ANNALS OF CARNEGIE MUSEUM

VOL. 63, NUMBER 1, P. 1-48 22 FEBRUARY 1994

GEOGRAPHIC VARIATION AND SYSTEMATICS OF THE STRIPED WHIPSNAKES (*MASTICOPHIS TAENIATUS* COMPLEX; REPTILIA: SERPENTES: COLUBRIDAE)

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ABSTRACT

Geographic variation in morphological and protein characters in *Masticophis taeniatus* sensu lato and *Masticophis bilineatus* were investigated. Populations of striped whipsnakes in southern Texas and eastern Mexico allocated to *M. t. schotti, M. t. ruthveni,* and *M. t. australis* are not conspecific with those of *M. t. taeniatus* and *M. t. girardi* of the western United States and Mexico. The southeastern populations are elevated to specific status and referred to *Masticophis schotti,* whereas the western whipsnake populations remain *M. taeniatus.* Striped whipsnake populations in south-central Mexico allocated to *M. t. australis* are not separable from those making up *M. t. ruthveni* and the two taxa are synonymized. *Masticophis schotti* and *M. taeniatus* differ from one another in maxillary tooth number, preanal dorsal scale row frequency, number of apical scale pits, and color pattern. An allelic difference across the Balcones Escarpment of central Texas at the supernatant amino acid transferase (*S-Aat-A*) locus exists between *M. t. girardi* and *M. s. schotti. Masticophis bilineatus* shows little geographic variation. A phylogenetic analysis of geographic samples supports the monophyly of both *M. taeniatus* and *M. schotti.*

RESUMEN

Se estudió la variación geográfica de caracteres morfológicos y protéicos en *Masticophis taeniatus* sensu lato y *Masticophis bilineatus.* Las poblaciones de las culebras rayadas en el sur de Texas y este de México, ante conocidas como *M. t. schotti, M. t. ruthveni,* y *M. t. australis* no son conespecíficas con *M. t. taeniatus* y *M. t. girardi* del oeste de Estados Unidos y México. Las poblaciones del sureste son elvadas a la categoría de especie y referidas como *Masticophis schotti,* mientras que las poblaciones del oeste retienen el nombre de *M. taeniatus.* Las poblaciones del sur del centro de México, conocidas como *M. t. australis,* las consideramos sinonimias con *M. t. ruthveni.* Estas dos especies difieren en el número de dientes maxilares, la frecuencia de líneas de escamas dorsales preanales, el número de foestas apicales y el patrón de coloración. Existe una diferencia en el locus del supernadante del aminoácido de transferencia (*S-Aat-A*) entre *M. t. girardi* y *M. s. schotti,* localizándose sobre el Balcones Escarpment del centro de Texas. *Masticophis bilineatus* presentó poca variación geográfica. Un análisis filogenético de las muestras geográficas sostiene la monofilia de *M. taeniatus* y *M. schotti.*

INTRODUCTION

The status of populations of the striped whipsnake, *Masticophis taeniatus* sensu lato, in Texas and Mexico has long been enigmatic to herpetologists. The first name applied to snakes of this species-group was *Leptophis taeniatus* (Hallowell, 1852). Striped whipsnakes from central and western Texas and western Mexico were described as *Masticophis ornatus* (Baird and Girard, 1853). This form was subsequently recognized as a subspecies of *M. taeniatus* (Cope, 1875). Stejneger

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Submitted 16 August 1991.

and Barbour (1917) did not recognize the genus *Masticophis* and relegated all species of *Masticophis* to *Coluber*. Hence they substituted *C. t. girardi* for *Coluber taeniatus ornatus*, which became a secondary junior homonym of *Coluber ornatus* Shaw, 1802 (=*Chrysopelea ornata* of Asia). Intergradation of color pattern characters between *M. t. taeniatus* and *M. t. girardi* was thought to occur in extreme western Texas (Ortenburger, 1928). Schmidt and Smith (1944) stated that the use of *Masticophis taeniatus ornatus* "appears to be in accord with the opinion of the International Commission on Zoological Nomenclature with regard to secondary homonyms." However, Article 59 of the 1985 Code stated that all secondary junior homonyms replaced before 1961 are permanently invalid; therefore, *M. t. girardi* should be used instead of *M. t. ornatus*.

Baird and Girard (1853) described *Masticophis schotti* from southern Texas, in the Tamaulipan Biotic Province. Ortenburger (1928) examined only three specimens of this taxon. Gloyd and Conant (1934) considered *M. schotti* a subspecies of *M. taeniatus*, based on two juvenile specimens that they believed to be intergrades from the eastern portion of the Edwards Plateau. A darker form with reduced striping from the lower Rio Grande valley of Texas and Tamaulipas, Mexico, described as *Masticophis ruthveni* (Ortenburger, 1923), was also considered a subspecies of *M. taeniatus* by Gloyd and Conant (1934). Based on the assumption that juvenile *M. t. ruthveni* do not have light stripes, Smith (1941) described *Masticophis taeniatus australis* from Guanajuato, Mexico.

Masticophis bilineatus was described by Jan (1863) from Mexico. Cope (1891) later applied the name *Bascanium semilineatum* to the same taxon from Arizona (Smith, 1941). Subspecies described include *Masticophis bilineatus lineolatus* (Hensley, 1950) from the Ajo Mountains of Arizona, based on minor color pattern differences, and *Masticophis bilineatus slevini* (Lowe and Norris, 1955), the putatively dwarf population on Isla San Esteban, Baja California, Mexico. Our interest in investigating geographic variation in *M. bilineatus* and the relationship of this taxon to *M. taeniatus* arose because of parapatry among similarly-patterned *M. bilineatus, M. t. girardi*, and *M. t. ruthveni* in south-central Mexico, and the apparent sympatry of *M. bilineatus* and *M. t. taeniatus* in central Arizona. The objectives of this study are to: (1) determine evolutionary relationships within the striped whipsnake complex, *Masticophis taeniatus* sensu lato; (2) determine evolutionary and geographic relationships between *Masticophis bilineatus* and *M. taeniatus*; and (3) document patterns of geographic variation in morphological and protein characters of *M. taeniatus* and *M. bilineatus*.

Materials and Methods

A total of 1633 *Masticophis taeniatus* and 335 *M. bilineatus* from throughout the ranges of these species was examined (Fig. 1, Appendix 1). The states for 36 characters were recorded for each *M. taeniatus*, and 35 for each *M. bilineatus*. Four measurements (total length, tail length, head length [snout to posterior margin of the last supralabial], and greatest head width) were recorded to nearest 0.1 mm. Because the character has been used to discriminate among subspecies of *M. bilineatus* (Lowe and Norris, 1955), the length of the right posterior chin shield divided by the distance from the anterior edge of the mental scute to the posterior edge of the posterior chin shield was calculated for *M. bilineatus*. The following data were also recorded: sex; age (adult or juvenile); anal plate condition (single/divided); number of scale rows at neck, midbody, and ten ventral scutes anterior to the vent (Dowling, 1951); numbers of supralabials, infralabials, preoculars, postoculars, loreals, primary temporals, secondary temporals, ventrals, subcaudals, and maxillary teeth; and supralabials contacting the orbit. Head scale variation is presented for the right side of the head only. Fourteen color pattern characters were also recorded. Presence and width (both dorsally and laterally) of a light nuchal collar

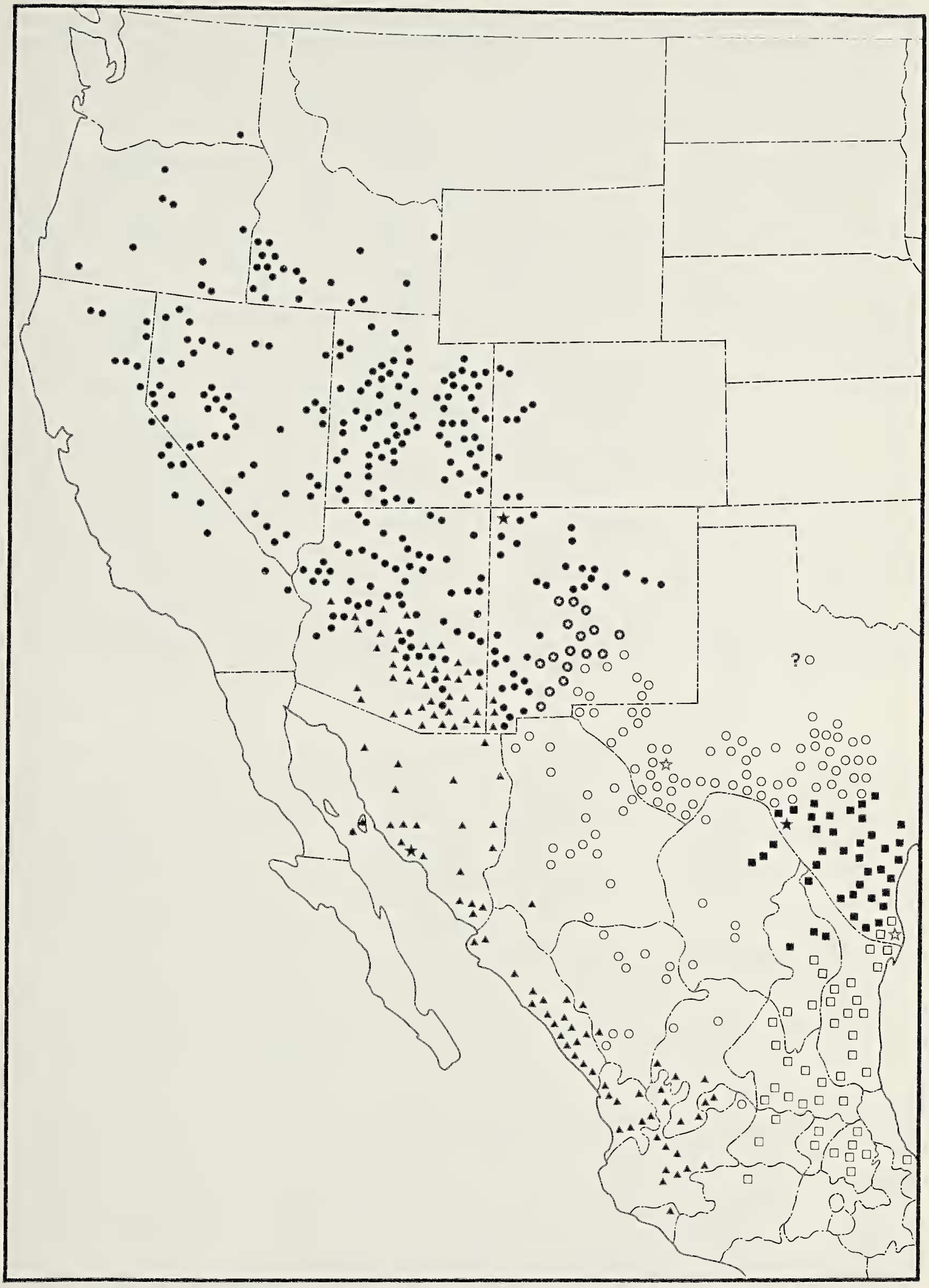

Fig. 1.—Map showing location of specimens examined in this study. Closed circles = *Masticophis t. taeniatus*, open circles = *M. t. girardi*, circled stars = *M. t. taeniatus* × *girardi*, black squares = *M. t. schotti*, open squares = *M. t. ruthveni*, and triangles = *Masticophis bilineatus*. Stars indicate type localities for respective taxa.

and number of light bands were recorded for *M. taeniatus* only. Other color pattern characters included: number of stripes; stripe color (light or dark); stripe position (scale row location); presence of dorsal speckling; presence of light head scale borders; dorsal color pattern; ventral pattern of neck, belly, and tail; and length of stripes expressed in numbers of ventral scutes. Scale row reductions were recorded for each specimen and presented in the formula recommended by Dowling (1951). The length of the inverted hemipenis was recorded in terms of subcaudals subtended.

Measurements were used to calculate five ratios: tail length/snout–vent length (TLR), head length/head width (HR), head length/snout–vent length (HLSVL), head width/snout–vent length (HWSVL), and posterior chin shield/mental–posterior chin shield distance (CSR, *M. bilineatus* only). Tests of geographic variation used analysis of variance (ANOVA) and Duncan's multiple range (univariate) and canonical discriminant analyses (multivariate) employing the GLM and CANDISC procedures of the Statistical Analysis System software package, respectively (SAS Institute, 1985). A significance level of $\alpha = 0.05$ was used on all statistical tests. Phenograms based on distance and correlation coefficient matrices were generated with the unweighted pair-group method using arithmetic means (UPGMA) algorithm of the Numerical Taxonomy System of Multivariate Statistical Programs, NT-SYS (Rohlf et al., 1980). Version 2.4 of Phylogenetic Analysis Using Parsimony (PAUP) and the associated CONTREE were used to perform phylogenetic analyses (Swofford, 1985). Genotype data were analyzed with Biosys-I computer software (Swofford and Selander, 1981).

Sexual, phylogenetic, and geographic variation analyses were conducted on the 22 samples shown in Fig. 3. Samples 1–17 and 22 represent *M. taeniatus* sensu lato and 18–21 are *M. bilineatus*. Samples included mapped localities grouped in 80.5 km^2 unit areas delineated after examining the geographic distribution of locality data and considering major biogeographic boundaries. Cluster analysis of the 80.5 km^2 unit areas, using the UPGMA algorithm on separate sexes, yielded these 22 samples (Fig. 3).

Heart, liver, kidney, and skeletal muscle tissue removed from freshly sacrificed specimens of *M. taeniatus* sensu lato (33), and *M. bilineatus* (3) were used to analyze protein variation by horizontal starch gel electrophoresis (Harris and Hopkinson, 1976; Selander et al., 1971; Table 1). Data from *M. bilineatus* were not included in analyses because too few individuals were available to accurately estimate allozyme variation. Voucher specimens are deposited in the Texas Cooperative Wildlife Collections, University of Texas at El Paso, and New Mexico State University (Appendix 2).

RESULTS

Ontogenetic Variation.—Due to insufficient samples of juveniles, the description of ontogenetic variation is limited to color pattern differences between adults and hatchlings. The hatchling color pattern of *M. taeniatus* sensu lato is invariable throughout its range (Fig. 2). The holotype of *M. t. australis* also exhibited this pattern and is identical to all other juvenile specimens examined. Adult color patterns are shown in Fig. 13 (*taeniatus*), 15 (*girardi*), 17 (*schotti*), and 19 (*ruthveni*). The color pattern of *M. bilineatus* changes little ontogenetically; therefore, only adult color patterns are shown (Fig. 20).

Hatchling *M. taeniatus* have a ground color of dark olive green dorsally, with two white or cream lateral stripes. One stripe encompasses the lower half of scale row 1 and the lateral edges of the ventrals. The other stripe is on the upper half of scale row 3 and the lower half of scale row 4. The dorsal pattern is most similar to that of adult *M. t. schotti* or some *M. t. ruthveni,* differing only in ground color shade and absence of dorsal speckling. Hatchlings have a cream-colored venter with a narrow, diffuse dark olive lateral stripe forming the lower border of the lower light stripe. The medial portion of the venter is immaculate. Some hatchling *M. taeniatus* have paired black spots on the first five to ten ventral scutes. Spots may also be scattered on the chin shields and gular scales. Hatchlings are most similar to adult *M. t. taeniatus* in ventral color pattern.

Sexual Variation.—Eleven characters and snout–vent length (SVL) were tested for sexual variation (Table 2). Samples 4, 11, 15, 16 (*M. taeniatus*), and 18 (*M. bilineatus*) were chosen because they are the largest (Fig. 3). A lower limit of 500 mm SVL was chosen for adult size in analyses of SVL. Males had significantly larger body sizes than females in samples 11 and 18 (Table 2).

Table 1.—*Proteins examined, tissues of origin, and electrophoretic conditions yielding best resolution of* Masticophis taeniatus *allozymes. Mitochondrial and supernatant loci are denoted by M- and S- prefixes, respectively.*

Protein	Enzyme Commission number	Locus	Tissue	Electrophoretic conditions[a]
Aminopeptidase	3.4.11.1	*AP-A*	liver	A
Aspartate aminotransferase	2.6.1.1	*M-AAT-A*	liver	B
	2.6.1.1	*S-AAT-A*	liver	C
Creatine kinase	2.7.3.2	*CK-A*	muscle	D
	2.7.3.2	*CK-C*	muscle	C
Dihydrolipoamide dehydrogenase	1.8.1.4	*DDH-A*	liver	B
Esterase[b]		*EST-D*	liver	C
Fumarate hydratase	4.2.1.2	*FUMH-A*	liver	C
General protein		*GP-1*	muscle	C
Glucose-6-phosphate dehydrogenase	1.1.1.49	*G6PDH-A*	heart	C
Glutamate dehydrogenase	1.4.1.2	*GTDHP-A*	liver	C
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-A*	muscle	C
Isocitrate dehydrogenase	1.1.1.42	*M-IDH-A*	liver	C
	1.1.1.42	*S-IDH-A*	liver	C
Lactate dehydrogenase	1.1.1.27	*LDH-A*	liver	C
	1.1.1.27	*LDH-B*	liver	C
Malate dehydrogenase	1.1.1.37	*M-MDH-A*	liver	C
	1.1.1.37	*S-MDH-A*	liver	C
Mannose-6-phosphate isomerase	5.3.1.8	*MPI-A*	muscle	D
Peptidase[c]	3.4.–.–	*PEP-A*	liver	A
		PEP-B	liver	A
		PEP-C	liver	A
		PEP-S	liver	A
Phosphoglucomutase	5.4.2.2	*PGM-A*	muscle	C
	5.4.2.2	*PGM-B*	muscle	C
Proline dipeptidase	3.4.13.9	*PRO-A*	liver	A
Pyruvate kinase	2.7.1.40	*PK-A*	liver	C
Superoxide dismutase	1.15.1.1	*S-SOD-A*	liver	B
Xanthine dehydrogenase	1.1.1.204	*XDH-A*	liver	B

[a] A: Tris-HCl pH 8.5/borate pH 8.2; B: Discontinuous tris-citrate-borate (Poulik, 1957); C: Tris-citrate pH 8.0; D: Tris-citrate pH 7.0.
[b] The substrate used was methyl-umbelliferyl acetate.
[c] Substrates used were leucyl-alanine for Peptidase A and C, leucyl-glycyl-glycine for Peptidase B, and leucyl-leucyl-leucine for Peptidase S.

Mean ventral counts were greater for females in samples 15 and 16, and greater for males in sample 18 (Table 2). Males had significantly higher mean subcaudal counts than females (Table 2). Males in samples 11 and 15 had greater mean maxillary tooth counts than females. Males had relatively longer tails, as measured by TLR, in sample 11, whereas females had relatively longer tails in sample 15 (Table 2). Sexual variation was not found in HR, HLSVL, or HWSVL. Males in samples 11 and 15 had relatively longer heads (Table 2).

Males in samples 4, 11, 15, and 16 had significantly fewer posterior scale rows than females. *Masticophis taeniatus* sensu lato always has 15 scale rows anteriorly and at midbody. The first scale row reduction (SRR1) is lateral (scale row 3) and paired. Therefore, SRR1 reduces scale rows from 15 to 13, and is considered a

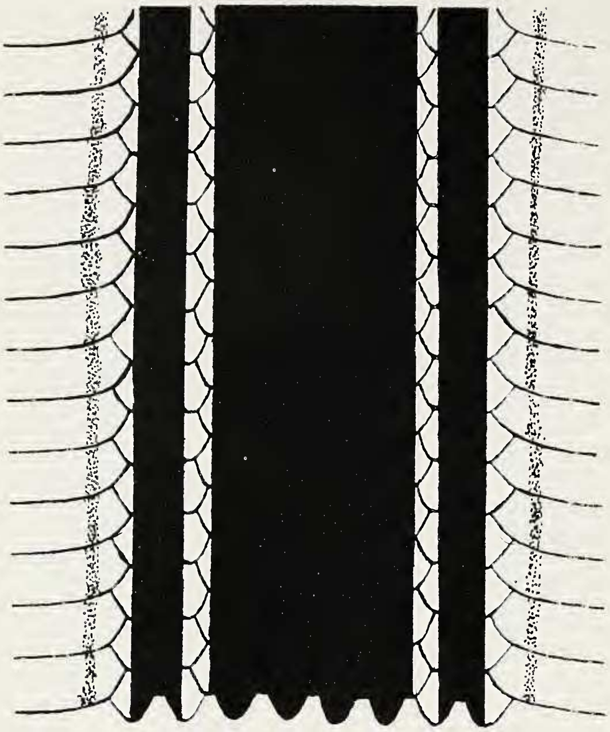

Fig. 2.—Color pattern of juvenile *Masticophis taeniatus* sensu lato.

single reduction site. The second (SRR2) and third (SRR3) reduction sites are unpaired, located middorsally, and occur separately. Most males in samples 4 (85%) and 11 (68%) had three scale row reduction sites (15-15-11, Table 2), whereas most females in these samples (80% and 69%, respectively) had two scale row reduction sites (15-15-12). Most males in samples 15 (57%) and 16 (48%) had two (15-15-12) scale row reductions (Table 2), whereas most females in samples 15 (75%) and 16 (84%) had one scale row reduction site (15-15-13). This is also illustrated by the small number of females in samples 15 and 16 with more than one scale row reduction site (Table 2). Females have a greater relative girth posteriorly as indicated by the more posteriad location of scale row reduction sites. The locations of all reduction sites were significantly different between the sexes in sample 11, but only SRR2 was significantly different in sample 4 (Table 2).

Virtually all *M. bilineatus* possess 17-17-13 scale rows. Scale row reduction 1 occurs laterally and is paired on scale row 4. The location of SRR2 and SRR3 were significantly different between the sexes in sample 18 (Table 2). Unlike the other four samples (*M. taeniatus*), males in sample 18 had SRR2 and SRR3 significantly more posteriad than did females.

Geographic Variation.—Geographic variation in ventral and subcaudal scutes was analyzed by plotting sample statistics on modified Dice-Leraas diagrams (Fig. 4–7). Samples with nonoverlapping shaded boxes (±2 SE) have means that are significantly different. Males in samples 15–17, 20, and 21 had significantly fewer mean ventrals than most in samples 1–14, 18, and 19 (Fig. 4). In females, samples

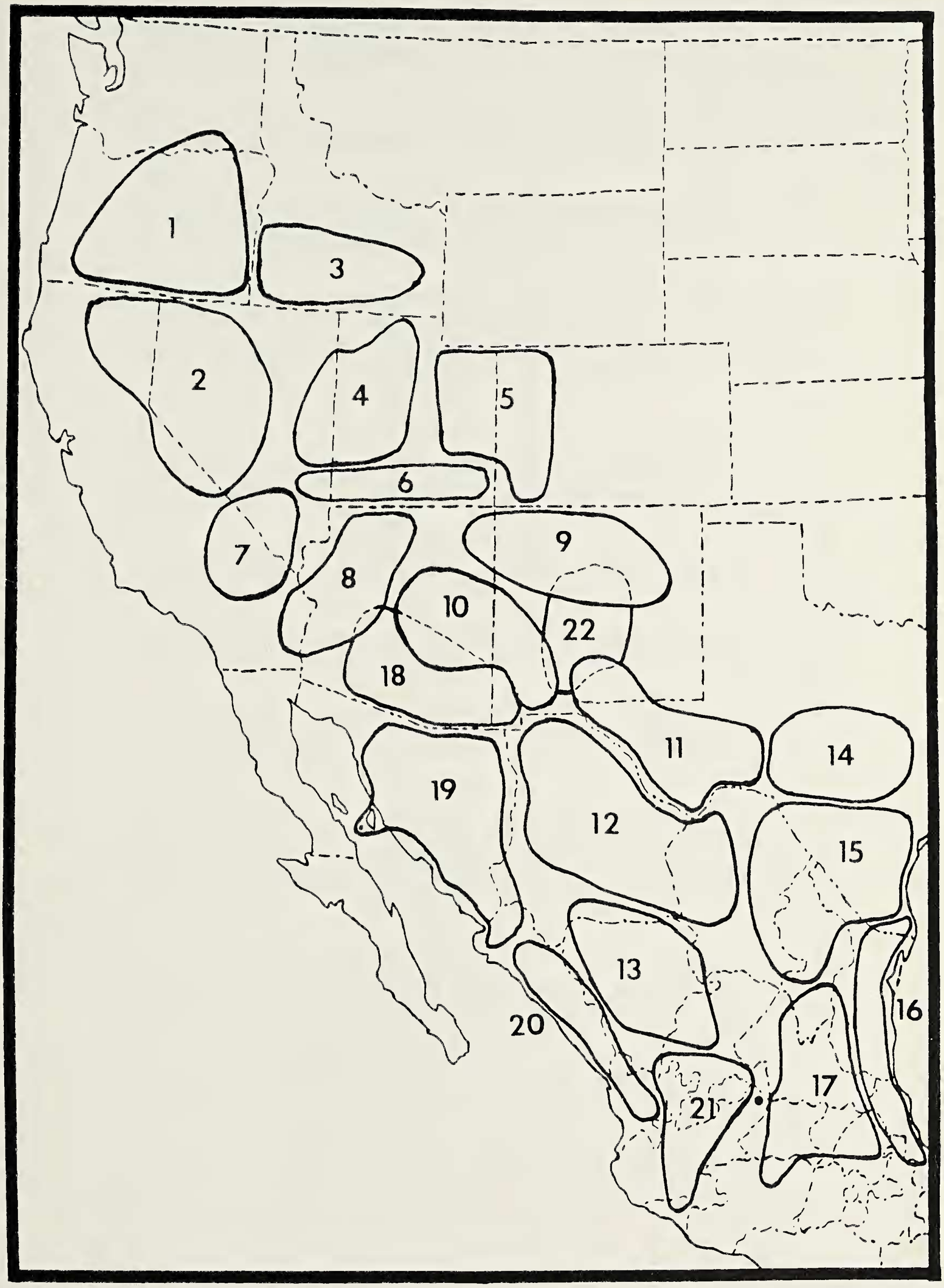

Fig. 3.—Distribution and location of the 22 samples of *Masticophis* used in this study. The locality between samples 17 and 21 is in sample 13 and is represented by one specimen only.

Table 2.—*Statistically significant (α = 0.05) sexual variation in samples 4, 11, 15, 16, and 18.*

Character	Sample	Males $\bar{x}$ (SD)	Males Range	Males SE	Males n	Females $\bar{x}$ (SD)	Females Range	Females SE	Females n	t
SVL[a]	11	930 (160.56)	511–1214	12.9	154	861 (143.25)	513–1166	14.3	101	3.58
	18	957 (173.09)	537–1353	18.8	85	870 (141.38)	356–1155	15.2	86	3.59
Ventrals[a]	15	196 (4.51)	181–206	0.53	72	200 (5.74)	188–213	0.80	52	−4.10
	16	193 (4.77)	183–203	0.76	39	196 (7.65)	184–213	1.53	25	−2.40
SC[a]	4	138 (8.46)	120–165	1.16	53	131 (5.63)	120–145	0.85	44	4.51
	11	150 (10.2)	131–175	0.97	112	147 (11.0)	105–178	1.41	61	2.12
	15	143 (8.93)	120–162	1.32	46	138 (9.79)	119–162	1.79	30	2.17
	16	143 (10.5)	129–160	2.61	16	135 (9.72)	113–152	2.81	12	2.07
	18	143 (9.58)	124–167	1.48	42	139 (8.06)	124–165	1.42	32	2.05
Maxillary teeth[b]	11	19.2 (1.02)	15–23	0.09	140	18.8 (0.90)	16–21	0.10	89	1.97
	15	17.4 (0.79)	16–19	0.10	69	17.3 (0.94)	16–20	0.14	48	1.98
TLR[b]	11	0.455 (0.107)	0.188–0.775	0.007	125	0.451 (0.081)	0.126–0.647	0.009	82	1.97
	15	0.453 (0.064)	0.180–0.572	0.007	88	0.430 (0.069)	0.228–0.517	0.009	61	1.98
HLSVL[b]	11	0.029 (0.002)	0.027–0.041	0.00	131	0.030 (0.003)	0.015–0.035	0.00	80	1.97
	15	0.033 (0.006)	0.018–0.051	0.001	76	0.032 (0.047)	0.026–0.050	0.001	53	1.98
Preanal scale rows[b]	4	11.1 (0.44)	9–12	0.05	72	11.8 (0.42)	11–13	0.05	61	1.98
	11	11.2 (0.54)	10–12	0.04	151	11.8 (0.51)	11–13	0.05	94	1.97
	15	11.8 (0.62)	11–13	0.07	76	12.7 (0.49)	11–13	0.07	55	1.98
	16	11.8 (0.70)	11–13	0.11	40	12.8 (0.50)	11–13	0.10	24	2.00
SRR1[a]	11	123 (7.55)	101–145	0.63	145	125 (6.53)	110–140	0.68	93	−2.50
SRR2[a]	4	128 (7.83)	110–154	0.92	72	136 (10.6)	116–173	1.40	58	−5.10
	11	131 (9.37)	110–158	0.78	145	139 (11.8)	119–180	1.27	86	−5.80
	18	124 (9.95)	91–167	1.11	84	121 (8.79)	93–154	1.00	82	2.12
SRR3[a]	11	160 (13.2)	127–195	1.30	103	166 (13.5)	139–187	2.70	25	−1.90
	18	135 (18.7)	113–192	2.41	60	127 (12.6)	95–189	1.55	66	2.91

[a] Student's t test on raw data.
[b] Wilcoxon Rank Sum test on raw data.

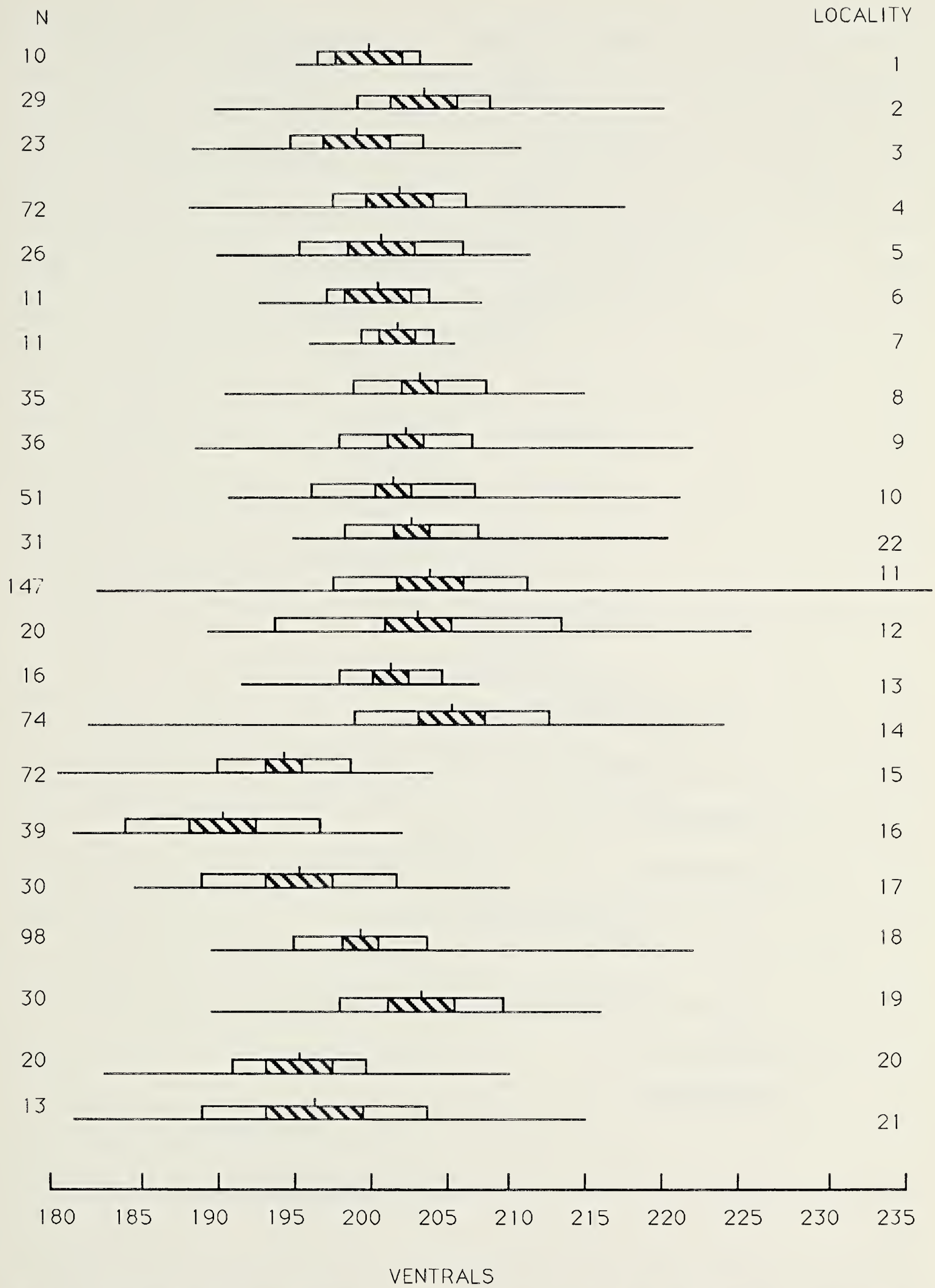

Fig. 4.—Modified Dice-Leraas diagram of geographic variation in ventrals of males of samples 1–22 shown in Fig. 3. Horizontal line is range, vertical line is mean, clear box is ±1 SD, and shaded box is ±2 SE.

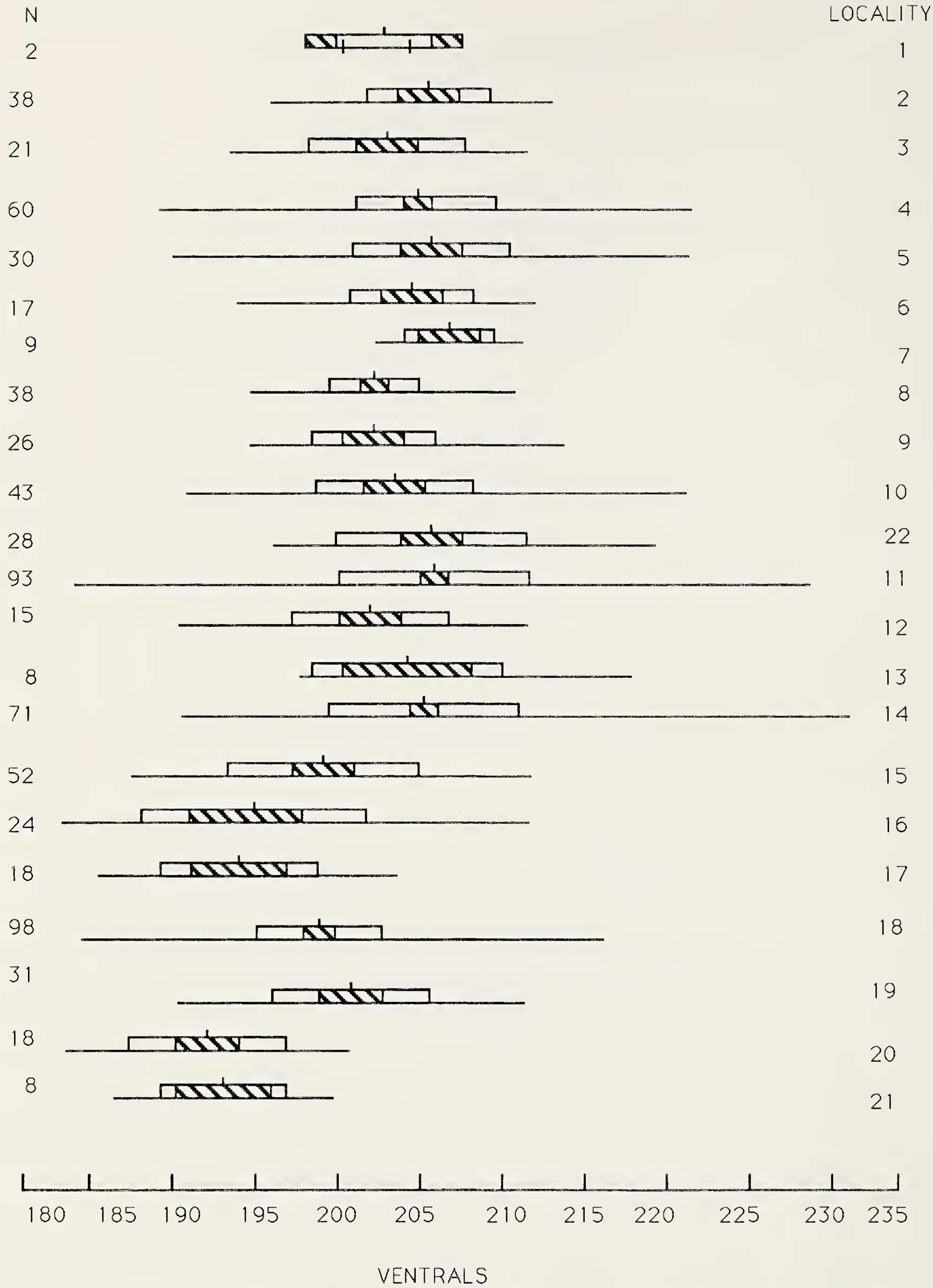

Fig. 5.—Modified Dice-Leraas diagram of geographic variation in ventrals of females of samples 1–22 shown in Fig. 3. Explanation as in Fig. 4.

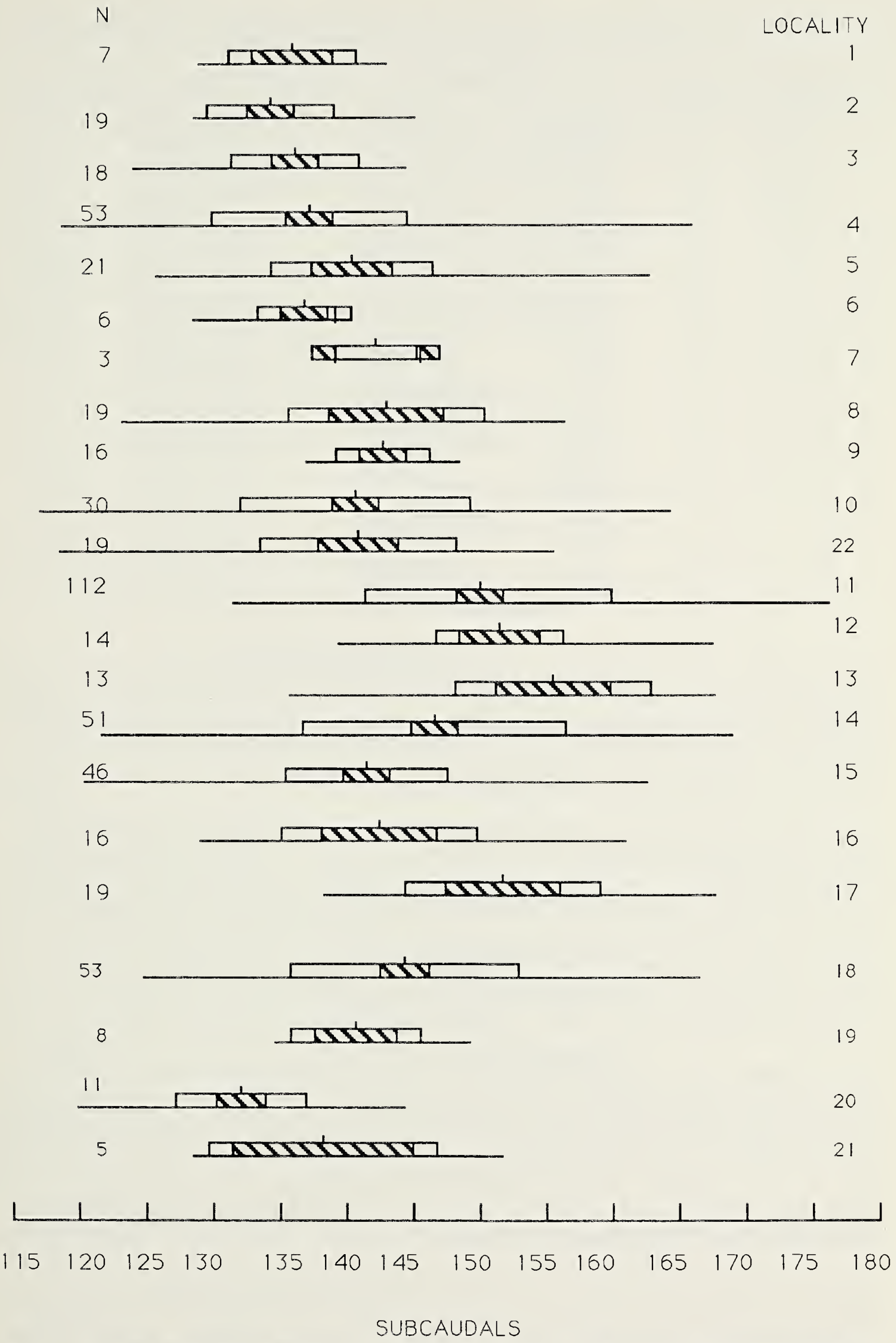

Fig. 6.—Modified Dice-Leraas diagram of geographic variation in subcaudals of males of samples 1–22 shown in Fig. 3. Explanation as in Fig. 4.

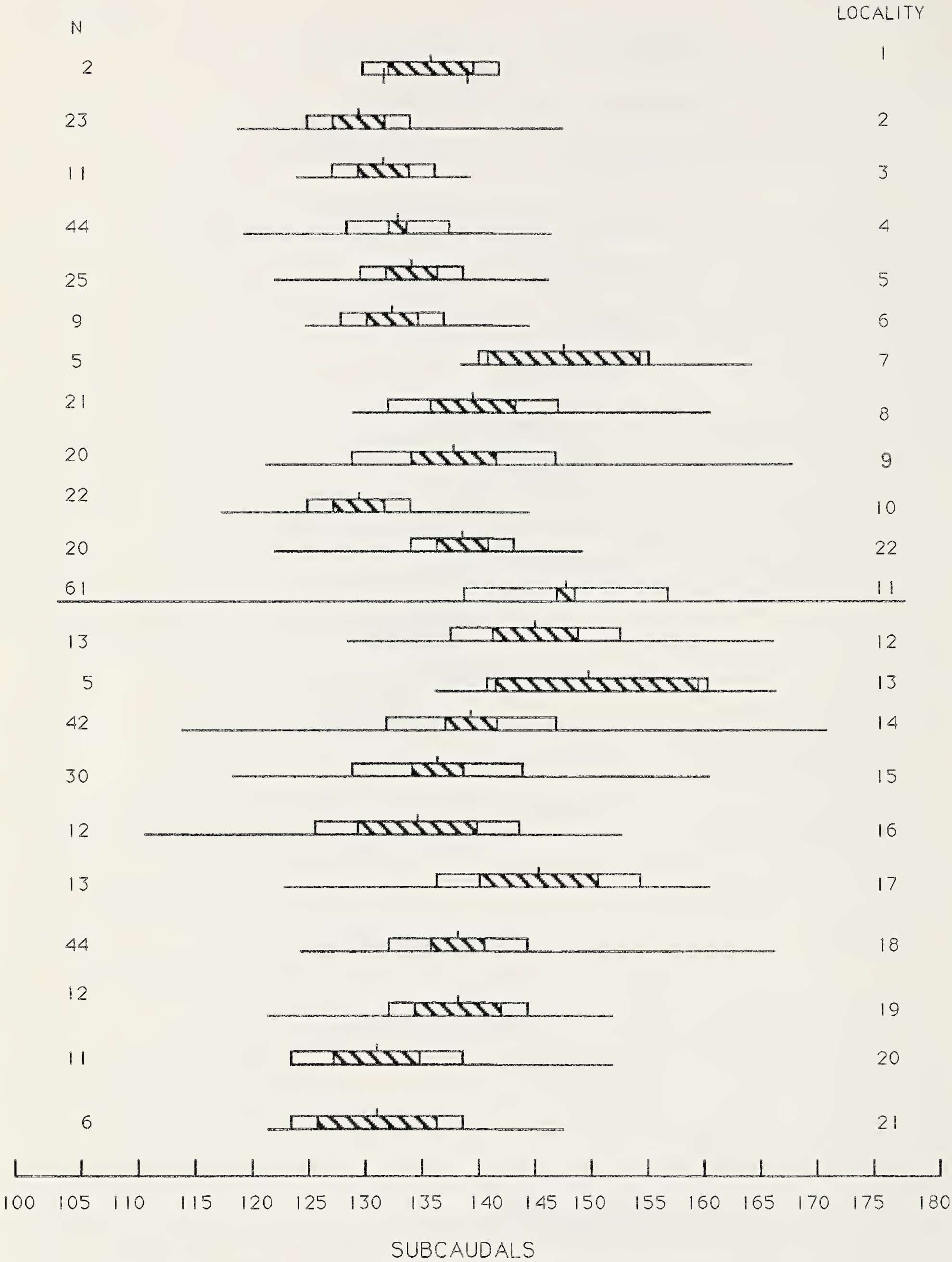

Fig. 7.—Modified Dice-Leraas diagram of geographic variation in subcaudals of females of samples 1–22 shown in Fig. 3. Explanation as in Fig. 4.

Table 3.—*Geographic variation in HLSVL among samples 1–22 shown in Fig. 3. Means of samples grouped by the same letter are not significantly different.*

n	$\bar{x}$ (SD)	Range	SE	Sample	Grouping
34	0.034 (0.002)	0.030–0.037	0.000	20	B
33	0.033 (0.002)	0.029–0.036	0.000	17	C
10	0.033 (0.002)	0.030–0.036	0.001	21	C
164	0.033 (0.002)	0.021–0.040	0.000	18	C
55	0.033 (0.003)	0.029–0.048	0.000	19	C
30	0.032 (0.002)	0.030–0.038	0.000	16	C F
20	0.031 (0.002)	0.028–0.035	0.000	13	D F
63	0.031 (0.002)	0.023–0.041	0.000	10	D F
28	0.031 (0.002)	0.027–0.039	0.000	12	A D F
60	0.030 (0.002)	0.025–0.036	0.000	8	A D E F
55	0.030 (0.003)	0.027–0.049	0.000	5	A D E F
35	0.030 (0.002)	0.018–0.037	0.000	15	A D E F
48	0.030 (0.002)	0.026–0.036	0.000	9	A D E F
19	0.030 (0.002)	0.028–0.034	0.001	7	A D E F
32	0.030 (0.002)	0.027–0.035	0.000	3	A D E F
56	0.030 (0.002)	0.027–0.035	0.001	22	A D E F
120	0.030 (0.002)	0.025–0.035	0.000	4	A D E F
60	0.030 (0.002)	0.027–0.035	0.000	2	A D E F
145	0.029 (0.002)	0.015–0.035	0.000	11	A E F
12	0.029 (0.001)	0.028–0.032	0.000	1	A E F
97	0.029 (0.004)	0.023–0.058	0.000	14	A E
27	0.029 (0.003)	0.018–0.034	0.001	6	E

16, 17, 20, and 21 had significantly fewer mean ventrals than most other samples (Fig. 5). However, ranges overlap extensively for both sexes. In both sexes there were significant differences in mean ventral counts between parapatric samples 14 and 15. The boundary between sample 14 (*girardi*) and sample 15 (*schotti*) forms the only contact zone between these taxa that is well-represented by specimens.

An increase in average subcaudal number in southern populations of males was evident among samples 1–13 and 15–17 (Fig. 6). A significant difference in mean subcaudal counts between samples 14 and 15 existed (Fig. 6). Sample 20 had a significantly lower mean subcaudal count than all other samples except 1, 2, and 21. A northwest to southeast clinal increase in subcaudals was present in females of samples 1–10 (Fig. 3, 7). Females in sample 22 (*M. t. taeniatus* × *M. t. girardi*) were intermediate between sample 10 (*taeniatus*) and sample 11 (*girardi*). A north to south clinal decrease in subcaudal number was evident among females in samples 14–16 and 18–21 (Fig. 3, 7).

ANOVAs were significant for hemipenis length, maxillary tooth counts, TLR, HR, HLSVL, and HWSVL. However, Duncan's multiple range tests showed significant variation in HLSVL only. Sample 20 had a significantly larger mean HLSVL ($P < 0.05$, d.f. = 1254, $n = 1255$). Samples grouped by the same letters have means that are not significantly different (Table 3). Samples 1–4, 15, and 17 had the largest mean hemipenis lengths; however, no significant groupings were found ($P < 0.05$, d.f. = 447, $n = 448$). Average maxillary tooth counts for samples 11–14 and 18–21 were greater than those for samples 1–10 and 15–17; however, no significant groupings were found ($P < 0.05$, d.f. = 693, $n = 694$). Samples 9, 11–13, and 16–17 had proportionately the longest tails, averaging >47% of SVL, whereas samples 1–4 had the lowest TLR values with averages

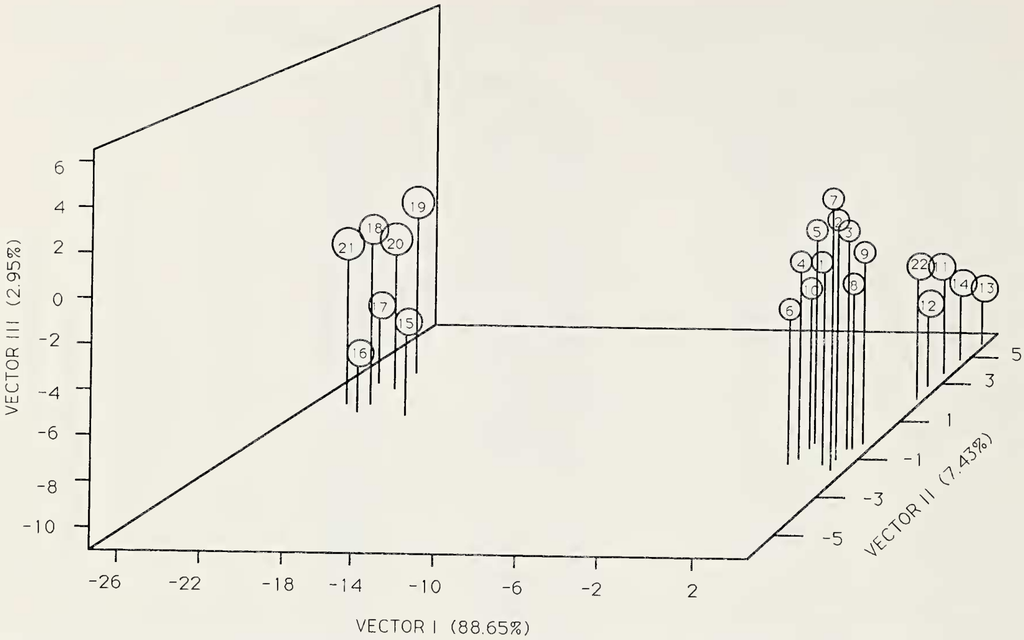

Fig. 8.—Projections on the first three canonical vectors of sample means of 22 samples of male striped whipsnakes, *Masticophis*.

≤44% of SVL. However, no significant groupings were found ($P < 0.05$, d.f. = 877, $n = 878$). No significant groupings of samples based on mean HR were found ($P < 0.05$, d.f. = 1252, $n = 1253$). Relative head width as measured by HWSVL was greater in southern samples, but no significant groupings were found ($P < 0.05$, d.f. = 1250, $n = 1251$).

Lowe and Norris (1955) implied that a lower CSR was characteristic of the insular and Ajo Mountains populations of *M. bilineatus*. Kruskal-Wallis tests comparing the Ajo Mountains population with four southern Arizona populations and southwestern New Mexico material were significant ($X^2 = 11.76$, $P < 0.05$, d.f. = 3). However, a Duncan's multiple range test comparing means of these populations showed no significant differences. A Kruskal-Wallis test showed no significant variation in CSR among samples 18–21 ($X^2 = 5.08$, $P > 0.05$, d.f. = 3). The population of *M. bilineatus* from Isla San Esteban did not differ significantly in SVL from three mainland Sonora populations (Kruskal-Wallis test, $X^2 = 3.02$, $P > 0.05$, d.f. = 3). The insular specimens were not significantly smaller, $t' = 0.981$, d.f. = 266, $P > 0.05$, with mean SVLs of 899 mm for 254 mainland adults and 854 mm for 14 adults from Isla San Esteban.

Multivariate analyses utilized the following characters: scale pit number, preanal scale rows, ventral counts, TLR, number of transverse light bands, number of stripes, maxillary tooth counts, HR, HLSVL, HWSVL, SRR1, and SRR2. A canonical discriminant analysis using Wilk's Lambda, Pillai's Trace, Hotelling-Lawley's Trace, and Roy's Greatest Root was conducted to test the null hypothesis of no overall significant variation due to locality. All were significant at $P < 0.05$. In the canonical discriminant analysis, canonical vectors I–III explained most (99.03%) of the variation (Table 4). Samples 1–14 and 22 separated from samples

Table 4.—*Eigenvalues and percent influence for 12 canonical vectors for the 22 samples of male striped whipsnakes,* Masticophis *shown in Fig. 3.*

Canonical vector	Eigenvalue	Percent influence	Cumulative
I	75.5058	88.65	88.65
II	6.3298	7.43	96.08
III	2.5133	2.95	99.03
IV	0.2564	0.30	99.33
V	0.1852	0.22	99.55
VI	0.1440	0.17	99.72
VII	0.0849	0.10	99.82
VIII	0.0487	0.06	99.88
IX	0.0442	0.05	99.93
X	0.0252	0.03	99.96
XI	0.0196	0.02	99.98
XII	0.0152	0.02	100.00

15–21 along canonical vector I which summarized 88.65% of the variation (Fig. 8; Table 4). Number of stripes was the most influential character along this axis (Table 5). Canonical vector II accounted for 7.43% of the variation and separated samples 1–10 from 11–14 and 22. Band number influenced this axis greatly (Table 5). Canonical vector III accounted for 2.95% of the variation and separated samples 15–17 from 18–21 (Fig. 8). Preanal dorsal scale row counts and SRR2 position influenced this vector the most (Table 5).

The patterns of separation seen in the canonical discriminant analysis were concordant with cluster analysis (Fig. 9). Characters used in cluster analysis included: scale pit number, number of scale rows around the anterior body, preanal scale rows, ventral counts, subcaudal counts, hemipenis length, number of transverse bands, number of stripes, maxillary tooth counts, TLR, HR, HLSVL, HWSVL, SRR1, SRR2, and SRR3. Three distinct clusters separating at distance values >1.0 were found (Fig. 9). Samples 1–14 and 22 form the largest cluster, with samples 15–17 and 18–21 forming two smaller clusters, respectively. Western samples 1, 2, and 7 grouped together, sample 22 grouped with the geographically proximate samples 9–10, but not with 11 or 12 (Fig. 3, 9). The significance of the relative position of sample 6 to samples 1–10 and the split among samples 11–14 is unclear, especially since neither were separated in Fig. 8.

Table 5.—*Variable coefficients for canonical variates I–III for 22 samples of male striped whipsnakes,* Masticophis.

Character	Vector I	Vector II	Vector III
Scale pit	0.1428	0.0817	0.1390
Preanal scale rows	−0.3550	0.1028	1.1623
Ventrals	0.0361	−0.0169	0.4014
TLR	−0.0304	0.0374	−0.2538
Bands	0.0732	2.6390	−0.1375
Stripes	8.2383	−0.9094	0.5162
Maxillary teeth	0.0420	0.2498	0.4193
HR	0.0460	−0.0912	0.0365
SRR1	−0.1404	0.1409	0.2080
SRR2	0.1767	−0.0922	−1.3304
HLSVL	0.0341	−0.0474	0.1031
HWSVL	0.0326	0.0412	−0.0650

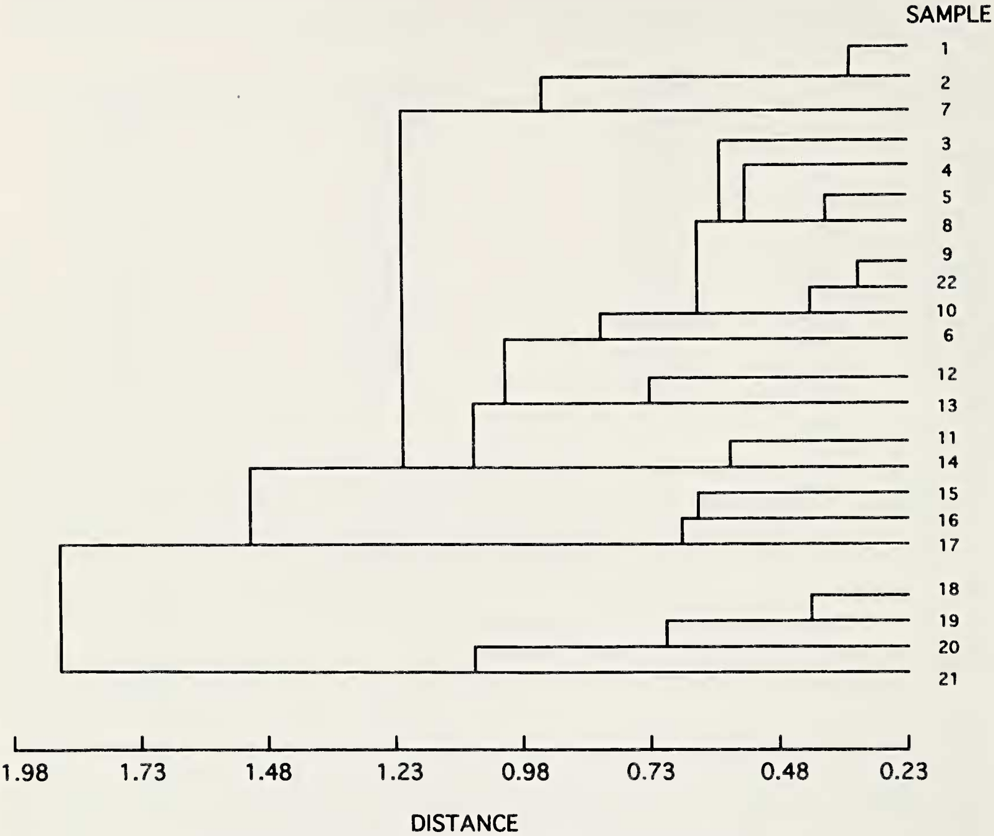

Fig. 9.—Phenogram based on UPGMA clustering of 16 morphological characters among 22 samples of male striped whipsnakes, *Masticophis*. Cophenetic correlation = 0.921.

A phylogenetic analysis based on the number of scale rows around the anterior body, preanal scale rows, number of transverse bands, number of stripes, scale pit number, dorsal speckling, head scale bordering, maxillary tooth counts, ventral counts, subcaudal counts, hemipenis length, and stripe color yielded the consensus tree shown in Fig. 10. Samples 18–21 were used for outgroup rooting. The mulpars option of PAUP version 2.4 produced nine most parsimonious trees 19 steps long with a consistency index of 0.842. Two monophyletic groups are evident, one consisting of samples 1–14 and 22 and another containing samples 15–17. Placement of samples within these groups and within the outgroup may not represent an accurate phylogenetic hypothesis due to the high probability of reticulate evolution among samples within groups (Thorpe, 1987). This tree differs from the phenogram (Fig. 9) in that sample 22 was placed with samples 11–14 and not samples 6 and 10. Otherwise the phylogenetic tree (Fig. 10) and the phenogram (Fig. 9) have similar topologies. The presence of 15 dorsal scale rows around the anterior body and at midbody is a synapomorphy uniting samples 1–17 and 22 within the *M. taeniatus* complex. Samples 18–21 have the pleisiomorphic condition of 17 scale rows around anterior and midbody.

Allozyme Variation.—The protein products of 29 presumptive gene loci were

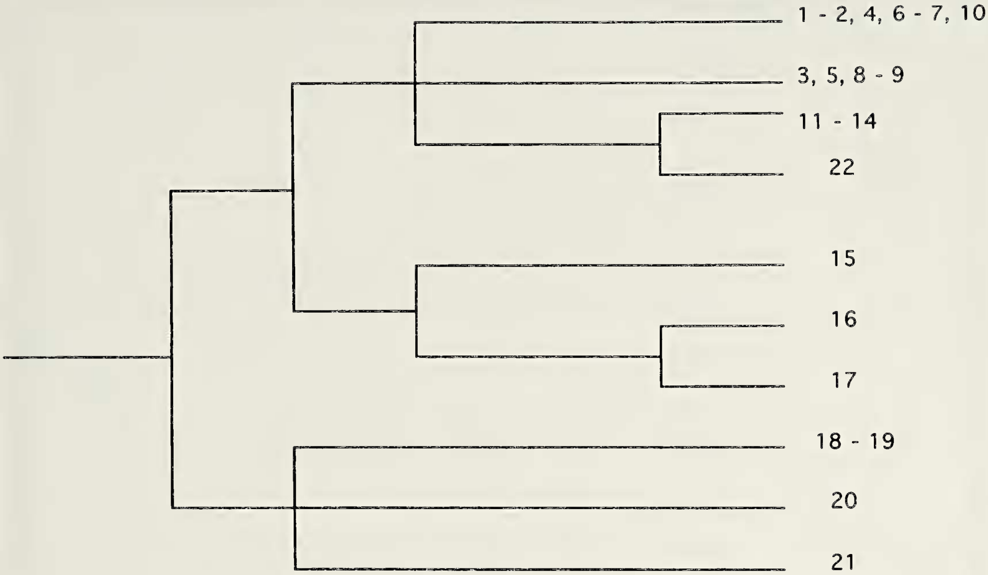

Fig. 10.—Phylogenetic tree of 22 samples of *Masticophis* shown in Fig. 3. Consistency index = 0.842.

assayed for variation in *M. taeniatus* sensu lato. Twelve of the 29 loci were polymorphic (Table 6). *Masticophis t. girardi* exhibited polymorphism at ten of the 12 variable loci. *Masticophis t. girardi* and *M. t. schotti* exhibited allelic differences in the *S-Aat-A* locus across their contact zone at the southern edge of the Balcones Escarpment (Fig. 11, Table 6). Both *M. t. taeniatus* and *M. t. girardi* are fixed for the *A* allele, while alleles *B* and *C* occur in *M. t. schotti* and alleles *A* and *C* are present in *M. t. ruthveni.* Neither an *M. t. girardi* (TCWC 64840), collected in Tamaulipan Biotic Province vegetation at the escarpment of the Edwards Plateau in Uvalde County, Texas, nor an *M. t. ruthveni* (TCWC 65282) from Brownsville, Texas, exhibited any protein activity at the *S-Aat-A* locus. The *A* allele was found in only one specimen of *M. t. ruthveni* from Hidalgo County, Texas, approximately 350 km south of the contact zone. The *M-Aat-A* locus also exhibited variation. The *B* allele was present at all *M. t. girardi* localities represented by more than one specimen, except the Brewster County and El Paso County, Texas, samples. This allele was also present in the homozygous state in a specimen of *M. t. taeniatus* from Socorro County, New Mexico, near the intergradation zone.

Genetic identity values were highest between *M. t. ruthveni* and both *M. t. taeniatus* and *M. t. girardi* (Table 7). The greatest genetic distances were between the parapatric *M. t. girardi* and *M. t. schotti* for all three measures used (Tables 7, 8). Even though *M. t. ruthveni* had *S-Aat-A* allele *A,* it clustered with *M. t. schotti* and not *M. t. taeniatus* or *M. t. girardi* (Fig. 12).

In addition to the results of morphological and allozyme analyses, additional evidence supporting differentiation of samples 15–17 from samples 1–14 and 22 is the absence of a broad intergradation zone between samples 14 and 15, such as the one seen in sample 22 (see systematic accounts). Only eight specimens exhibited intermediate morphological character states between samples 11–14

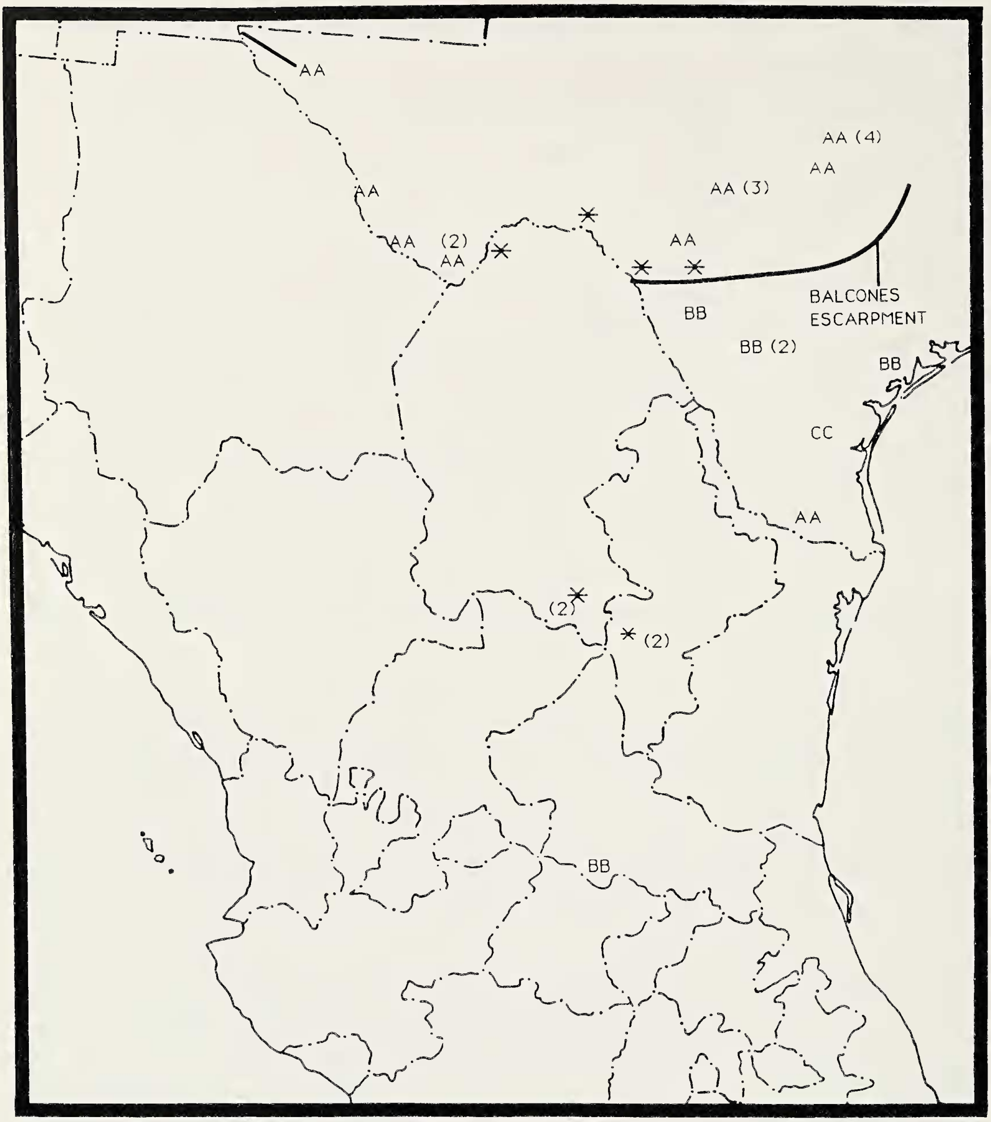

Fig. 11.—Distribution in Texas and Mexico of genotypes of the *S-Aat-A* locus and morphological hybrids. Location of hybrids denoted by an asterisk, numbers are sample sizes per locality.

and 15–17 (Fig. 11). The Balcones Escarpment contact zone between samples 14 and 15 is well-represented by specimens. Only four putative hybrids were found there (Fig. 11). Four specimens having intermediate color patterns were found at three localities in Mexico. These may represent a contact zone running northwest to southeast between samples 12 or 13 and 15 or 17 in southeastern Coahuila and western Nuevo Leon, respectively. They are considered putative hybrids, even though the nearest localities for samples 12 and 13 are in central Coahuila and central Zacatecas, respectively. This gap may be a collecting artifact. In ca-

Table 6.—*Allele frequencies at 12 polymorphic loci examined in the subspecies of* Masticophis taeniatus.

Locus and allele	*M. t. taeniatus*	*M. t. girardi*	*M. t. schotti*	*M. t. ruthveni*
S-Aat-A				
n	4	16	5	2
A	1.000	1.000		0.500
B			0.800	0.500
C			0.200	
M-Aat-A				
n	6	19	5	3
A	0.833	0.632	1.000	1.000
B	0.167	0.316		
C		0.053		
Ck-A				
n	6	16	2	3
A	1.000	0.937	1.000	1.000
B		0.062		
Ck-C				
n	6	14	2	3
A	1.000	0.929	1.000	1.000
B		0.071		
Ddh-A				
n	6	18	5	3
A	1.000	0.899	1.000	1.000
B		0.111		
Est-D				
n	6	15	5	3
A	1.000	0.967	1.000	1.000
B		0.033		
Gapdh-A				
n	5	16	5	3
A	0.800	0.937	1.000	1.000
B	0.200	0.062		
S-Idh-A				
n	6	17	5	3
A	1.000	0.971	1.000	1.000
B		0.029		
Mpi-A				
n	5	16	2	3
A	1.000	0.937	1.000	1.000
B		0.062		
Pep-S				
n	6	18	5	3
A	1.000	1.000	0.800	1.000
B			0.200	
Pgm-A				
n	6	16	3	3
A	1.000	0.969	1.000	1.000
B		0.031		
Pk-A				
n	4	14	4	2
A	1.000	0.964	1.000	1.000
B		0.036		

Table 7.—*Matrix of Nei's (1972) genetic identity above the diagonal and genetic distance below, calculated from the 29 loci examined for the subspecies of* Masticophis taeniatus.

Population	1	2	3	4
1 *taeniatus*	*****	0.997	0.967	0.989
2 *girardi*	0.003	*****	0.963	0.986
3 *schotti*	0.034	0.038	*****	0.992
4 *ruthveni*	0.011	0.014	0.008	*****

nonical discriminant analysis, the eight presumed hybrids did not have variable coefficients either similar to one another or intermediate between parental forms. Instead, Edwards Plateau hybrids grouped with either samples 1–10 or 16–17. The Nuevo Leon hybrids grouped with samples 11–14 and the Coahuila hybrids grouped with samples 1–10. These specimens show a disharmonic combination of character states typical of interspecific hybrids (Lawson and Lieb, 1990). We consider this strong evidence of severely restricted gene flow between samples 14 and 15 across the Balcones Escarpment, and of reproductive isolation of these samples. The results of phylogenetic analyses show that two monophyletic groups exist (Fig. 10), one contains samples 1–14 and 22 and the other contains samples 15–17. Therefore, samples 1–10 are considered to be *Masticophis taeniatus taeniatus* and samples 11–14 *Masticophis taeniatus girardi,* with sample 22 containing specimens intermediate between them. These appear to be reproductively isolated from sample 15, which is *Masticophis schotti schotti,* and samples 16–17, which are *Masticophis schotti ruthveni.* Samples 18–21 correspond to *Masticophis bilineatus.*

SYSTEMATICS

Masticophis taeniatus (Hallowell)

Leptophis taeniata Hallowell, 1852:181. Holotype: USNM 2110; adult male (547 mm SVL); collected by Dr. S. W. Woodhouse, date unknown. Type locality: New Mexico west of the Rio Grande; restricted to Shiprock, San Juan Co., New Mexico, USA (Smith and Taylor, 1950). See Parker (1982) for synonymies.

Definition.—A species of whipsnake with 15 anterior and midbody dorsal scale rows; four dark stripes, one in the center of each of the first four dorsal scale rows (Fig. 13); and dorsal head plates edged in cream or white (Fig. 14). Transverse light gray bands are present in some specimens (Fig. 15). All specimens lack paired light speckling on the dorsal scales and red or pink pigment immediately posterior to the angle of the jaw. Two subspecies, *M. t. taeniatus* and *M. t. girardi,* are recognized (see subspecies accounts).

Table 8.—*Matrix of Rogers' (1972) genetic distance, below the diagonal, and Cavalli-Sforza and Edwards (1967) chord distance, above the diagonal, calculated from the 29 loci examined for the subspecies of* Masticophis taeniatus.

Population	1	2	3	4
1 *taeniatus*	*****	0.090	0.190	0.117
2 *girardi*	0.026	*****	0.209	0.145
3 *schotti*	0.051	0.068	*****	0.115
4 *ruthveni*	0.030	0.046	0.022	*****

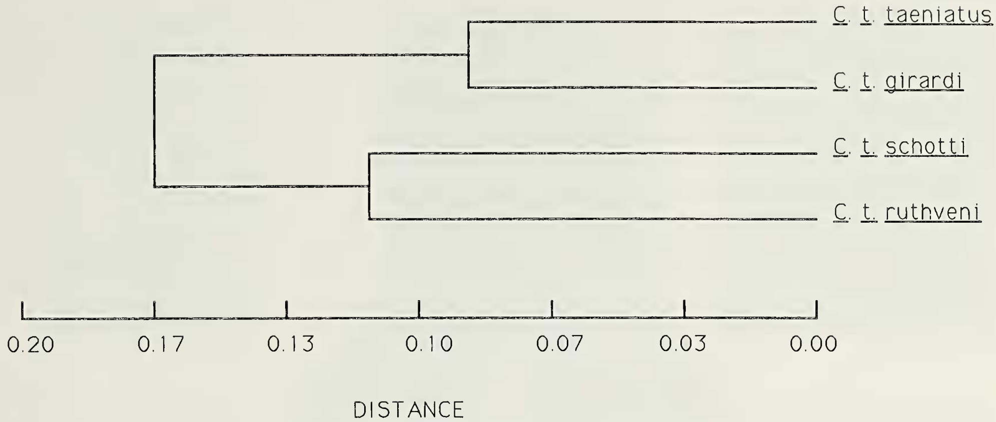

Fig. 12.—Phenogram showing the relationships of the subspecies in *Masticophis taeniatus* sensu lato, based on UPGMA of Cavalli-Sforza and Edwards (1967) chord distance from Table 14. Cophenetic correlation = 0.714.

Variation.—See Table 9 for meristic variation. Variation in primary and secondary temporal scales included 39 different arrangements in *M. taeniatus*. The lower primary temporal scale was divided, 3-2 pattern, in 531 (43.2%) specimens. No divisions, 2-2 pattern, were found in 423 (34.4%) specimens. All other temporal scale arrangements occurred at a frequency of <5%. No geographic component to temporal scale variation was found.

The number of scale row reduction sites ranged from one (15-15-13) to five (15-15-9) in both sexes of *M. taeniatus*. Most males (473, 70.9%) had three (15-

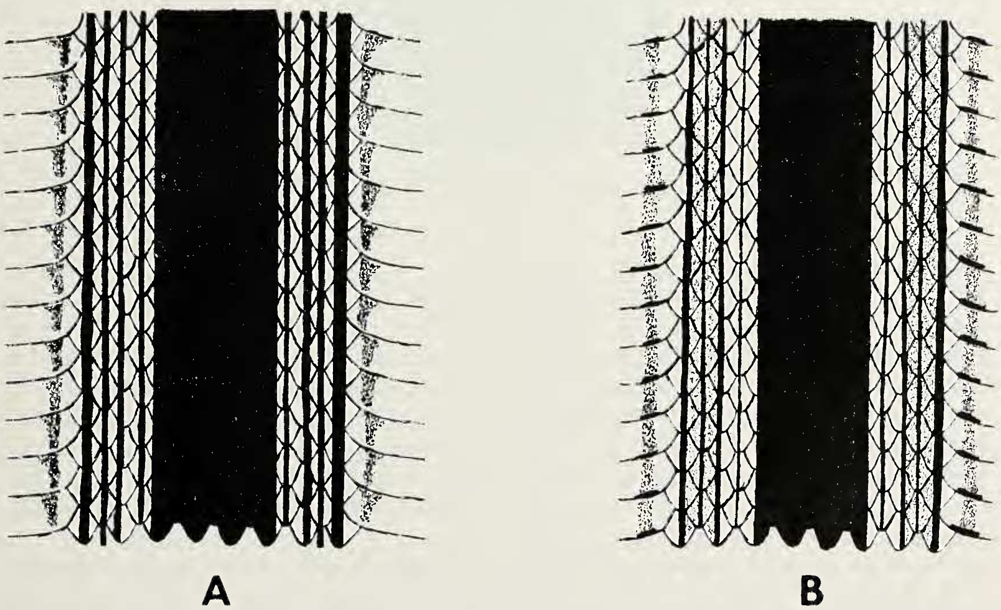

Fig. 13.—Color pattern of adult *Masticophis taeniatus taeniatus*: A) pattern found throughout subspecies' range; B) pattern found in the southern portion of its range and in smaller specimens.

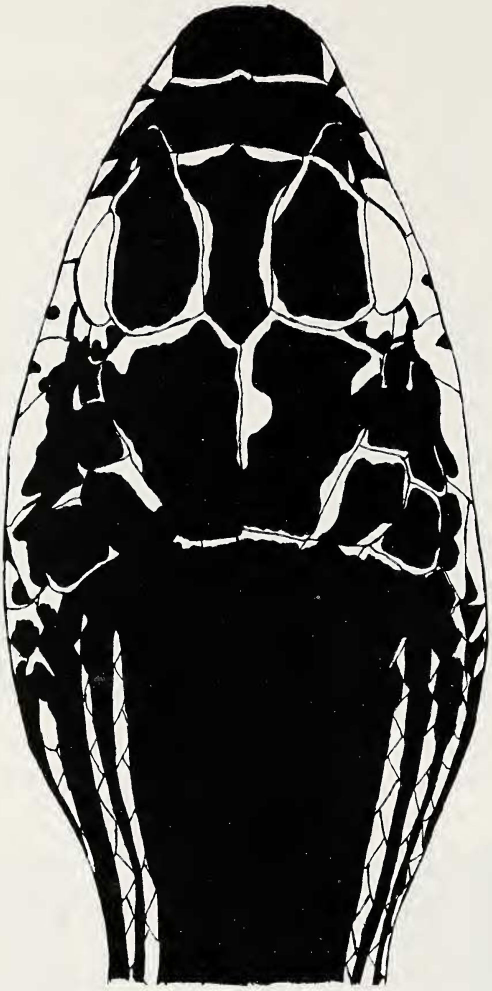

Fig. 14.—Head color pattern of adult *Masticophis taeniatus taeniatus.*

15-11) reduction sites, whereas most females (446, 75.7%) have only two (15-15-12). Two reduction sites were present in 168 (25.2%) males and three reduction sites were present in 122 (20.7%) females. One reduction site (15-15-13) was present in five (0.8%) males and 17 (2.9%) females. Three (0.5%) females and 19 (2.9%) males had four reduction sites (15-15-10). Five reduction sites (15-15-9), were present in only two (0.3%) males and one (0.2%) female. Variation in SRR1 for males: $\bar{x}$ = 121 (91–151, n = 643); females: $\bar{x}$ = 122 (95–146, n = 576). Variation in SRR2 for males: $\bar{x}$ = 132 (109–175, n = 633); females: $\bar{x}$ = 139 (112–180, n = 546). Variation in SRR3 for males: $\bar{x}$ = 159 (118–206, n = 460); females: $\bar{x}$ = 164 (123–190, n = 119).

Distribution.—This species is found in the Great Basin and Chihuahuan deserts and the Edwards Plateau of Texas (Fig. 1). *Masticophis taeniatus* occurs north to the Snake and Columbia river valleys of Idaho and Washington, respectively. It occurs east of the Cascade Mountains, Oregon, the Sierra Nevadas, California,

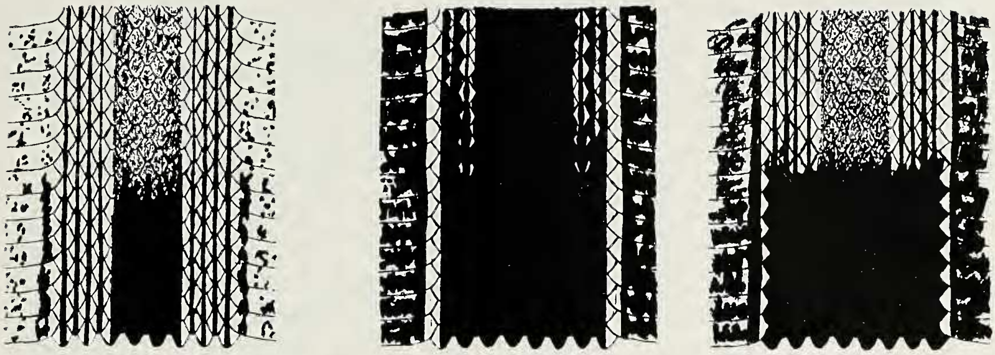

Fig. 15.—Color patterns of adult *Masticophis taeniatus girardi*: A) light pattern common throughout the Chihuahuan Desert; B) dark pattern common on the Edwards Plateau; C) intermediate pattern found throughout the subspecies' range.

and the Continental Divide in Mexico. It is absent from the Wasatch and Uinta mountain ranges in Utah. In Arizona, *M. taeniatus* is found mainly north of the Gila River. It ranges east into extreme western Colorado and to the Llano Estacado in eastern New Mexico, and south to northeastern Jalisco, Mexico. The eastern and southern range limits of *M. taeniatus* in Mexico are poorly understood.

The subspecies of *M. taeniatus* intergrade along the upper Rio Grande valley in central New Mexico (sample 22). Specimens exhibiting intermediate color patterns have been found from the vicinity of Albuquerque south to Las Cruces. This intergradation zone may be widest at the southern end, stretching from Carlsbad Caverns National Park, Eddy County, west to eastern Grant County. However, this may be an artifact of collecting because records are lacking from northern Catron, southern Valencia, and western Socorro counties in west-central New Mexico. Intergrades have a striping pattern similar to that shown in Fig. 13B, with 0–8 ($\bar{x}$ = 4) faint transverse bands present anteriorly. Remnants of the nuchal collar, characteristic of *M. t. girardi* (Fig. 15), occur in most intergrades. The back, head, and stripes are usually dark gray or brown. The venter is more heavily pigmented than in most *M. t. taeniatus,* but less so than in *M. t. girardi.* Thirty-seven male and 31 female intergrades were examined.

Masticophis taeniatus taeniatus (Hallowell)
(Fig. 13, 14)

Definition and Diagnosis.—The desert striped whipsnake, *M. t. taeniatus,* has 15 dorsal scale rows anteriorly and at midbody, light borders on head scales, and four dark longitudinal stripes. It is the only *Masticophis* with 15 dorsal scales rows lacking transverse bands, dark ventral mottling, light dorsal speckling, and red pigment at the angle of the jaw. *Masticophis t. taeniatus* has fewer subcaudals and maxillary teeth than *M. t. girardi.*

Distribution.—*Masticophis t. taeniatus* has primarily a Great Basin Desert distribution (Fig. 1). It occurs south into southwestern New Mexico east of the Continental Divide. Its range slightly overlaps the range of *M. bilineatus* across central and southeastern Arizona. *Masticophis t. taeniatus* does not occur in Mexico or Texas, contrary to what Ortenburger (1928), Parker (1982), and Conant

Table 9.—*Meristic variation among* Masticophis taeniatus, M. schotti, *and* M. bilineatus. *An asterisk indicates a modal value for that character and a plus sign indicates that supralabials 4 and 5 contact the eye.*

Characters		*M. taeniatus*			*M. schotti*			*M. bilineatus*		
		$\bar{x}$ (SD)	Range	*n*	$\bar{x}$ (SD)	Range	*n*	$\bar{x}$ (SD)	Range	*n*
Ventral	M	204 (7.0)	183–236	647	195 (5.8)	181–212	170	200 (6.9)	182–221	163
	F	205 (6.3)	187–232	575	198 (6.6)	181–218	120	199 (6.3)	183–216	157
SC	M	144 (10.6)	117–175	472	145 (9.1)	120–166	106	141 (9.1)	120–167	79
	F	138 (10.8)	105–178	393	139 (9.6)	113–162	77	137 (8.7)	121–165	73
Maxillary teeth		18.3 (1.2)	15–23	1196	17.5 (1.0)	15–21	268	19.3 (0.8)	17–23	300
Hemipenis length (SC)		8.7 (1.8)	4–15	420	8.8 (1.5)	6–13	81	8.0 (1.6)	5–14	103
Supralabials+		8*	7–9	1229	8*	6–9	290	8*	7–9	321
Infralabials		9*	8–11	1229	9*	8–10	289	9*	8–11	321
Preoculars		2*	1–3	1229	2*	1–3	289	2*	none	321
Postoculars		2*	1–3	1229	2*	1–3	289	2*	2–4	321
Loreals		1*	1–2	1251	1*	1–3	305	1*	1–2	309
Scale pits		2*	0–3	1229	1*	0–3	289	1*	0–2	321

and Collins (1991), report. Only two specimens from Washington were examined (Appendix 1) and additional localities (Nussbaum et al., 1983) for Washington were not confirmed. The specimen from near Oakland, Alameda County, California (CAS 10639) is a *M. t. taeniatus,* but we believe its locality data are incorrect.

Color Pattern Variation.—This subspecies shows little variation in color pattern. The head, back, and stripes are usually dark olive green, but may be brown to almost black in some southern specimens. In many smaller, presumably younger specimens and those from the southern part of its range, lateral stripes 2 and 4 are lighter than stripes 1 and 3, with a slight darkening between stripes 1 and 3 (Fig. 13B), but the pattern depicted in Fig. 13A is most common. The head plates are edged with light pigment (Fig. 14). In life, the posterior quarter of the venter and entire ventral surface of the tail are pink. The rest of the venter is usually cream with a blurry stripe on the lateral portions of the ventrals (Fig. 13). More than 90% of each sample has black spotting on the lower jaw, throat, and neck regions (Fig. 3). Northern specimens have dark ventral pigment occurring at high frequencies; samples 1–3 (32%–46%). Dark ventral pigmentation occurs at frequencies of <15% in all other samples except sample 9 (39% with dark ventral pigment). This may be due to the influence of *M. t. girardi.*

Masticophis taeniatus girardi (Stejneger and Barbour) (Fig. 15, 16)

Masticophis ornatus Baird and Girard, 1853:102. Holotype: USNM 1971; skin of adult, sex unknown, collected by J. D. Graham, date unknown. Type locality: USA, Texas, between San Antonio and El Paso; restricted to Fort Davis, Jeff Davis Co. (Smith and Taylor, 1950). See Parker (1982) for synonymies.

Coluber taeniatus girardi Stejneger and Barbour, 1917:89.

Diagnosis.—The central Texas whipsnake, *M. t. girardi,* differs from *M. t. taeniatus* in having transverse light banding, darker dorsal and ventral coloration, and higher subcaudal and maxillary tooth counts. It lacks the dorsal light flecking and red pigment at the angle of the jaw that are present in *M. schotti.*

Distribution.—*Masticophis t. girardi* has a Chihuahuan Desert–western Mexican Plateau distribution with an eastward extension onto the Edwards Plateau of Texas (Fig. 1). The hiatus in the range of *M. t. girardi* in southern Coahuila, northern Zacatecas, and northwestern San Luis Potosi, Mexico, may be a sampling artifact. The western boundary of the range follows the continental divide with a few localities west of it in Durango and northeastern Jalisco, Mexico. In central Texas, the range limits of *M. t. girardi* closely follow the Balcones Escarpment. A Throckmorton County, Texas, specimen (TNHC 26579) is typical *M. t. girardi,* but is so far out of range that its locality data are believed to be incorrect (Dixon, 1987).

Color Pattern Variation.—The dorsal head plates are light edged in all but the darkest specimens (Fig. 16). A light collar is present in all specimens, but is broken into two light nape blotches by dark pigment in 48.9% of specimens examined (Fig. 16). The lateral portions of the collar (nape blotches) range from one to five scales wide. Most specimens (42.3%) have nape blotches three scales wide, whereas 40.9% have them two scales wide. The medial collar width ranges up to five scales, with 48.9%, 23.3%, 14.0%, and 10.7% having a medial collar width of zero, one, two, and three scales wide, respectively. Dorsal light bands, posterior to the collar, range from zero to ten, averaging 5.3 in 479 specimens. No geographic variation in band number was found.

Fig. 16.—Head color pattern of adult *Masticophis taeniatus girardi.*

The dorsal color patterns illustrated in Fig. 15 represent the ends of a continuum of variation. Fig. 15C represents a common intermediate condition. Pattern 15A differs from 15C in that some light areas are present between stripes, especially stripes 3 and 4. Color patterns were scored as belonging to one of these three

Table 10.—*Dorsal color pattern frequencies found among samples 11–14 of* Masticophis taeniatus girardi *shown in Fig. 3. Pattern types refer to Fig. 15.*

	Pattern		
Sample	Light (15A)	Dark (15B)	Intermediate (15C)
11	64.70%	16.81%	18.48%
12	81.08%	2.70%	5.41%
13	88.00%	4.00%	8.00%
14	13.70%	60.27%	15.34%

patterns (Fig. 15). The light pattern (Fig. 15A) is more common throughout the Chihuahuan Desert (samples 11–13, Table 10). The dark pattern (Fig. 15B) is dominant on the Edwards Plateau (sample 14), occurring at low frequencies in samples 11–13. Specimens scored as intermediates (Fig. 15C) were most common in the northern part of the range (samples 11 and 14) and occur at low frequencies in samples 12–13 (Table 10). The anterior ventral pattern of *M. t. girardi* consists of black pigment covering >50% of the chin shields, gulars, and anterior ventrals in >99% of specimens. The belly is mostly black in >92% of specimens. The subcaudals have dark pigment confined to the lateral edges in >88% in samples 11–14 (Fig. 3). The posterior quarter of the venter and the subcaudals are pink in life. In dark specimens, the pink may be reduced to only the small areas between the dark blotches on the ventrals.

The predominance of the dark pattern (Fig. 15B) on the Edwards Plateau may be associated with thicker vegetation such as *Juniperus.* Five melanistic specimens of *M. t. girardi* were found. One such Edwards Plateau specimen is an adult female 1090 mm SVL (CAS 103476) from Val Verde County, Texas. Three additional specimens (CM 48192, LACM 116256, and KU 80828) are from the Cuatro Cienegas basin in central Coahuila, Mexico (Camper and Dixon, 1990). Another specimen (KU 39567) is an adult female (938 mm SVL) from western Coahuila, Mexico.

Masticophis schotti (Baird and Girard)

Masticophis schotti Baird and Girard, 1853:160. Holotype: USNM 1972, adult male (943 mm SVL) collected by Arthur Schott, date unknown. Type locality: Eagle Pass, Maverick Co., Texas, USA. See Parker (1982) for synonymies.

Definition.—The only species of *Masticophis* with 15 anterior and midbody dorsal scale rows, paired white, cream, or yellow spots on the anterior corners of the dorsal scales, uniformly dark head plates, and red pigment immediately posterior to the jaw angle. Two subspecies, *M. s. schotti* and *M. s. ruthveni,* differ from one another primarily in color pattern. See subspecies accounts for descriptions of type specimens and color patterns.

Variation.—See Table 9 for meristic variation. Thirty-one temporal scale patterns were found. The nondivided 2-2 pattern was the most frequent, 35.3% (102 specimens). The lower primary was divided, 3-2 pattern, in 69 (23.9%) specimens. The lower primary and secondary temporals were fused in 33 (11.4%) specimens. Other temporal scale arrangements existed at frequencies <5% with no geographic variation discernible.

The number of scale row reduction sites ranged from one (15-15-13) to four (15-15-10) in males and from one to three (15-15-11) in females. Most males (96, 54.9%) had two (15-15-12) reduction sites, whereas most females (97, 74.1%) had only one (15-15-13). Two reduction sites were present in 30 (22.9%) females and one reduction site was present in 24 (13.7%) males. Three reduction sites (15-15-11) were present in 53 (30.3%) males and four (3.1%) females. Two (1.1%) males had four reduction sites (15-15-10). Variation in SRR1 in males: $\bar{x}$ = 119 (88–139, n = 165); females: $\bar{x}$ = 117 (76–138, n = 118). Variation in SRR2 in males: $\bar{x}$ = 151 (112–184, n = 137); females: $\bar{x}$ = 157 (115–186, n = 30). Variation in SRR3 in males: $\bar{x}$ = 159 (136–190, n = 49); females: $\bar{x}$ = 161 (154–172, n = 4).

Distribution.—This species is found from the Balcones Escarpment of central Texas south to the Gulf Coastal Plain and inland onto the Mexican Plateau (Fig. 1). The western limits of its range in northern Mexico are unclear.

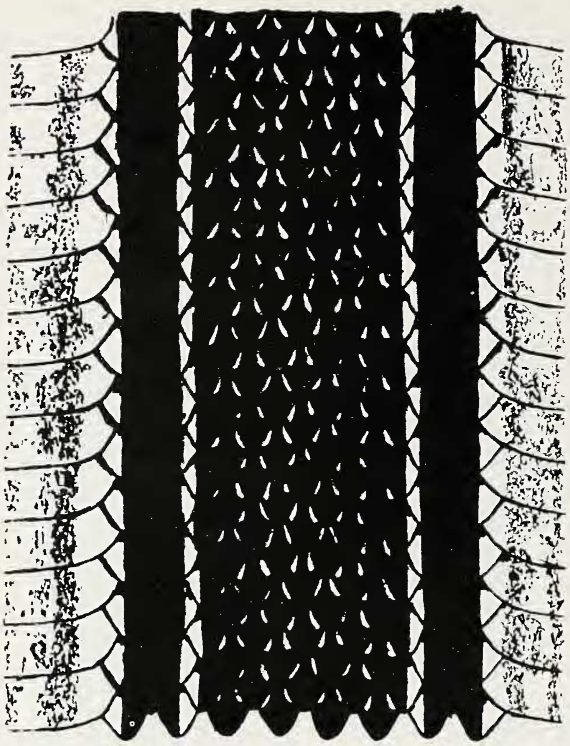

Fig. 17.—Color pattern of adult *Masticophis schotti schotti.*

Masticophis schotti schotti (Baird and Girard),
new combination
(Fig. 17, 18)

Definition and Diagnosis.—Masticophis s. schotti has 15 anterior and midbody dorsal scale rows, paired cream-colored light spots on the anterior dorsal scale corners and invariably two prominent light stripes. It differs from *M. s. ruthveni* in having lighter ground color, lighter dorsal speckling, and a more prominent upper light stripe that always extends past ventral 110.

Distribution.—The geographic range of *M. s. schotti* is apparently restricted to the Tamaulipan Biotic Province of Blair (1949; Fig. 1). Few specimens from Mexico exist, and the western range limits in the Coahuila Folded Belt Region are unclear.

Color Pattern Variation.—Adult *M. s. schotti* are invariant in color pattern (Fig. 17). The grayish-green ground color does not fade in preservative. In life, the subcaudals are pink in most specimens, except for their lateral tips which are grayish-green. Grayish-green speckling is present on the subcaudals in 15.0% of *M. s. schotti* examined. The red pigment behind the jaw angle fades in preservative.

Masticophis schotti ruthveni (Ortenburger),
new combination
(Fig. 18, 19)

Masticophis ruthveni Ortenburger, 1923:2. Holotype: UMMZ 57681, adult male (1104 mm SVL), collected by A. I. Ortenburger, date unknown. Type locality: Brownsville, Cameron Co., Texas, USA. Paratypes: UMMZ 57682–57684 and 57686–57694, UIMNH 43493, and MCZ 62561.

Fig. 18.—Head color pattern of adult *Masticophis schotti* and *Masticophis bilineatus.*

Masticophis taeniatus australis Smith, 1941:390. Holotype: USNM 10240, juvenile female, collected by A. Duges in 1879. Type locality: "Guanajuato," Guanajuato, Mexico. New synonymy.

Definition and Diagnosis.—Ruthven's whipsnake, *M. s. ruthveni,* has 15 anterior and midbody dorsal scale rows, paired dorsal spotting, and a variable color pattern. Because the holotype of *M. t. australis* is a typical juvenile *M. s. ruthveni,* we herein synonymize the former. It differs from *M. s. schotti* in having narrower, fainter stripes that are variable in number, darker dorsal spots, and a more variable ground color that is usually darker. The upper light stripe does not extend to ventral 110.

Distribution.—*Masticophis s. ruthveni* is found on the Gulf Coastal Plain from the Rio Grand south to central Veracruz, Mexico (Fig. 1). Gaps along the east coast of Mexico in Tamaulipas and Veracruz are believed to result from collecting bias. This taxon ranges west into the Sierra Madre Oriental and onto the southern part of the Mexican Plateau west to northern Michoacan. The western range limits of *M. s. ruthveni* are unclear. Two putative *M. t. girardi* × *M. s. ruthveni* hybrids

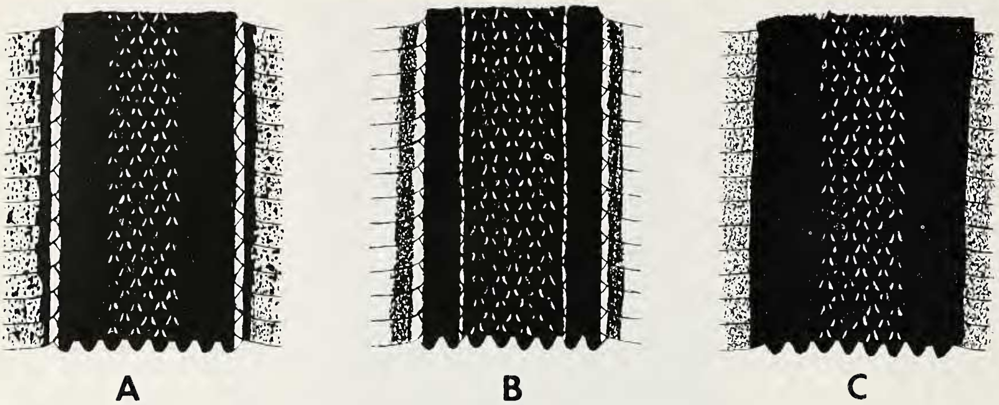

Fig. 19.—Color patterns of adult *Masticophis schotti ruthveni*: A) two-striped pattern most common throughout the subspecies' range; B) four-striped pattern found uncommonly throughout the subspecies' range; C) rare stripeless pattern.

from central Nuevo León indicate that *M. s. ruthveni* may not occur as far west in northern Mexico as it does on the southern part of the Mexican Plateau. In the USA, this subspecies occurs in Cameron, Hidalgo, Starr, Willacy, and south central Kenedy counties, Texas. The juvenile identified as *M. s. schotti* by Martin (1958) from La Joya de Salas, Tamaulipas, Mexico, (UMMZ 110818) is a *M. s. ruthveni,* as is UIMNH 3836 from 25 miles south of Monterrey, Nuevo León, Mexico (Shannon and Smith, 1949).

Color Pattern Variation.—Specimens exhibiting only the lower light stripe were the most common, occurring at a frequency of 56.8% (Fig. 19A; Table 11). Two light stripes were found in 37.5% of *M. s. ruthveni* (Fig. 19B). The upper light stripe, occurring on the upper margin of scale row 3 and lower margin of scale row 4, is narrow and faint. It extended as far posterior as ventral 110 (*M. s. schotti* character state) in only four (3.5%) *M. s. ruthveni.* The 5.8% of *M. s. ruthveni* that lacked stripes had a dark olive, almost black, ground color with bright yellow dorsal speckling (Fig. 19C). Stripeless specimens occur in southern Tamaulipas and eastern and southwestern San Luis Potosi, Mexico. Little geographic variation in color pattern was found. The frequencies of the one- and two-striped morphs are equal in the lowland sample 16 (Table 11). The ventral color pattern varies from dense speckling on the lateral quarter of the ventrals to sparse speckling toward the ventral midline, except in stripeless specimens, where dense ventral speckling is present throughout. The venter is the same color as the dorsum in striped specimens. In stripeless specimens, it is lighter toward the midline. Dorsal

Table 11.—*Dorsal color pattern frequencies found among samples 16–17* Masticophis schotti ruthveni *shown in Fig. 3. Pattern types refer to Fig. 19.*

Pattern	Sample 16	Sample 17
1-stripe (19A)	42.86%	67.80%
2-stripes (19B)	42.86%	22.03%
0-stripes (19C)	14.29%	10.17%

pigment extends ventrally to the lateral subcaudal tips. Medially, the subcaudals are pink in living specimens.

Masticophis bilineatus Jan
(Fig. 18, 20)

Masticophis bilineatus Jan, 1863:65. Holotype: MTKD 15523, female (467 mm SVL), date of collection and collector unknown. Type locality: Restricted to Guaymas, Sonora, Mexico (Smith and Taylor, 1950). Restriction of type locality to Casas Grandes, Chihuahua by Schmidt (1953) is in error (see remarks).

Bascanium semilineatum Cope, 1891:626. Holotype: USNM 1981, female, 816 mm SVL, collected by A. Schott, date unknown. Type locality: Colorado River bottom, Arizona.

Zamenis semilineatus: Gunther, 1894:121.

Bascanion semilineatum: Van Denburgh, 1896:347.

Coluber semilineatus: Stejneger and Barbour, 1917:80.

Masticophis semilineatus: Ortenburger, 1923:2.

Coluber bilineatus: Bogert and Oliver, 1945:362.

Masticophis bilineatus lineolatus Hensley, 1950:272. Holotype: UIMNH 5611, male, 1011 mm SVL, collected by M. Hensley, 23 May 1949. Type locality: North branch of Alamo Canyon, Ajo Mountains, 12.9 mi S and 5 mi E of the Ajo–Tucson–Sonoyta junction, Pima Co., Arizona. New synonymy.

Masticophis bilineatus slevini Lowe and Norris, 1955:93. Holotype: SDNHM 3826, female, 833 mm SVL, collected by Mrs. G. Bancroft, 18 April 1930. Type locality: Isla San Esteban, Gulf of California, Sonora, Mexico. New synonymy.

Definition and Diagnosis.—*Masticophis bilineatus* is the only striped *Masticophis* with a combination of 17 anterior and midbody dorsal scale rows, two dark lateral stripes on each side of the body, and paired light spots on the anterior corners of the dorsal scales. Because the previously described subspecies do not differ from other populations in the characters on which their descriptions were based, we herein synonymize them with *M. bilineatus*. It differs from *M. taeniatus* and *M. schotti* in having more dorsal scale rows. It differs from other striped whipsnakes that have 17 dorsal scale rows in dorsal ground color and by possessing paired light spots on the dorsal scales.

Description of Holotype.—Dorsal scale rows 17-17-13. A portion of the venter is missing and the tail is incomplete so ventral and subcaudal counts were not made. A paratype, (MTKD 15068) an adult female (748 mm SVL) has 196 ventrals, 130 subcaudals and 17-17-13 dorsal scale rows. The paratype has a dorsal scale row reduction formula as follows:

$$17 \frac{3 + 4(114)}{3 + 4(114)} 15 \frac{7 + 8(118)}{} 14 \frac{6 + 7(124)}{} 13\,(196)$$

Scale row reduction sites of the holotype involve the same dorsal scale rows as those of the paratype. The holotype has 20 maxillary teeth and one apical scale pit. It has a divided anal plate; supralabials 8-9; infralabials 11-10; preoculars 2-2; postoculars 2-2; and loreals 1-1. Supralabials 4 and 5 contact the right orbit and supralabials 5 and 6 contact the left orbit. Supralabial 3 on the left side is divided. Both right primary temporals are divided, 4-2 pattern, and all but the lower left secondary are split, 4-3 pattern.

The color pattern is characteristic for the species (Fig. 20B). Two dark stripes are present, the lower stripe is located on the lower half of scale row 1 and adjacent tips of the ventrals, and the upper stripe is located on the upper half of scale row 2 and lower half of scale row 3. The dorsal scales have paired light spots at their anterior corners. The dorsal coloration is dark olive green fading to light green

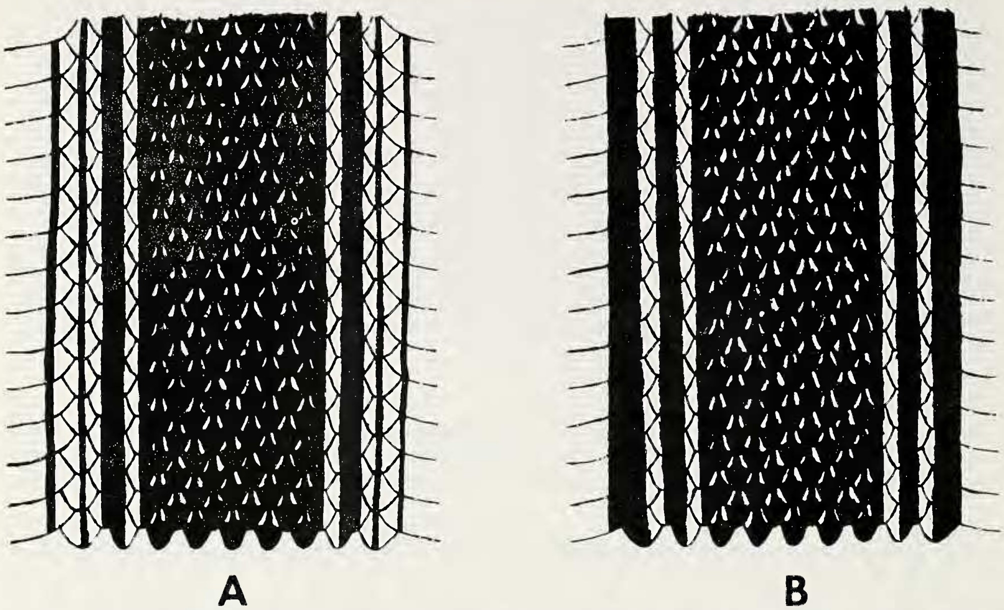

Fig. 20.—Color pattern of adult *Masticophis bilineatus*: A) lighter pattern more common in larger specimens; B) darker pattern more common in smaller specimens.

posteriorly. The light stripe between the upper dark stripe and the middorsum does not fade anterior to ventral 110. The head plates are uniformly colored the same shade as the dorsum (Fig. 18). The venter is immaculate except for the dark spots present on the chin shields, gulars, and first 10–15 ventrals. The subcaudals are also immaculate, except for their lateral tips, which are the same color as the dorsum.

Remarks.—We believe that Schmidt (1953) is in error in restricting the type locality of *M. bilineatus* to Casas Grandes, Chihuahua, Mexico. This locality is east of the continental divide where this species does not occur.

Variation.—See Table 9 for meristic variation. Thirty-one right temporal scale patterns were recorded for *M. bilineatus.* A divided lower primary, 3-2 pattern, occurred in 72 (22.4%), 64 (19.9%) had all but the lower secondary divided, 4-3 pattern. No temporals were divided in 52 (16.2%), both primary temporals were divided, 4-3 pattern, in 30 (9.4%). Other temporal scale patterns occurred at frequencies $<5\%$. No geographic component to temporal scale variation was found.

The number of scale row reduction sites ranged from two to five in males and from two to six in females. Most males (150, 91.5%) and females (155, 95.1%) had three reduction sites (17-17-13). Eleven (6.7%) males and five (3.1%) females had four (17-17-12) scale row reduction sites. One (0.6%) male and two (1.2%) females had only two (17-17-14) reduction sites. Two (1.2%) males had five (17-17-11) reduction sites and one (0.6%) female had six (17-17-10) reduction sites. Variation in SRR1 for males: $\bar{x} = 115$ (81–136, $n = 158$); females: $\bar{x} = 114$ (91–129, $n = 153$). Variation in SRR2 in males: $\bar{x} = 123$ (91–167, $n = 154$); females: $\bar{x} = 121$ (93–154, $n = 147$). Variation in SRR3 in males: $\bar{x} = 130$ (108–192, $n = 117$); females: $\bar{x} = 127$ (95–189, $n = 121$).

Distribution.—In the north, *M. bilineatus* has a Sonoran Desert distribution that interdigitates with that of *M. t. taeniatus* in eastern and central Arizona. Sympatric populations may occur in southwestern Yavapai County, western Gila County, and southern Graham County, Arizona. *Masticophis bilineatus* and *M. t. girardi* appear to be parapatric in western Durango and northern Jalisco, Mexico. In New Mexico, USA, and northern Sonora, southern Zacatecas, northern Jalisco, and Aguascalientes, Mexico, the eastern range limits of *M. bilineatus* follow the Continental Divide. From the Sonoran Desert it occurs south along the Gulf of California lowlands to Colima with an eastward range extension onto the Mexican Plateau in Jalisco, Aguascalientes, and Zacatecas. The specimen supposedly from Isla San Pedro Martir (UO 32528) is probably from Isla San Esteban (D. Hews, personal communication). Two specimens, both labelled MCZ 4582, from San Pedro, Coahuila, Mexico, are *M. taeniatus* and *M. bilineatus.* Since the latter is so far out of range, the locality data are believed to be incorrect. The same is true for USNM 46499, purportedly from Cuicatlam, Oaxaca, Mexico.

Color Pattern Variation.—The dorsal color pattern of *M. bilineatus* varies little, with both patterns present in specimens of all sizes and from all of its range (Fig. 20). The head plates of *M. bilineatus* are uniformly dark and identical in shade to the rest of the dorsum (Fig. 18). Pattern 20B is most common in smaller individuals, whereas pattern 20A is more common in larger specimens. An adult male (TCWC 21903, 733 mm SVL) from Mazatlán, Sinaloa, Mexico, has an aberrant color pattern. The light line between the upper dark stripe and the back is absent, forming a uniformly dark dorsum starting at the upper half of scale row 2 on each side. Dark pigment is present on the lateral tips of the ventrals and on the ventral and posterior edges of each scale in row 1, forming a narrow diffuse lower dark stripe. The paired cream-colored spots at the anterior corners of the dorsal scales are present in this and all adult *M. bilineatus.*

The ventral color pattern of *M. bilineatus* varies little, with dark spotting present on the chin shields, gulars, and first 10–15 ventrals in 131 (45.6%) specimens, and absent in 168 (54.4%). Ventral spots form a median row that usually extends 10–15 ventrals posterior to the head, but in the Isla San Esteban population it extends approximately 40 ventrals farther posteriorly. Dark spotting on the belly was present in only 37 (12.0%) specimens, whereas 272 (88.0%) lacked belly spotting. Dark spotting was present on the subcaudals of 137 (44.3%) *M. bilineatus,* 175 (55.7%) had dark pigment on the lateral subcaudal tips only. Subcaudal spotting occurred at a frequency of about 50% in samples 18 and 19, but was virtually absent from samples 20 and 21 (Fig. 3).

DISCUSSION

Masticophis taeniatus and *M. schotti* are well-differentiated morphologically. Many color pattern differences are obvious and were weighted highest by the canonical discriminant analysis (see species accounts). Additionally, *M. taeniatus* and *M. schotti* differ in a number of meristic and mensural character states. The differences are greatest between *M. t. girardi* and *M. s. schotti* across the southern Balcones Escarpment. They differ in *M. t. girardi* having a higher frequency of three SRR sites, two apical scale pits, higher maxillary tooth counts, significantly higher mean ventral counts, and significantly smaller mean HWSVL. The Balcones Escarpment is a well-known geographic boundary for many reptile species, including 37 species of snakes (Smith and Buechner, 1947). The occurrence of *M.*

t. girardi (TCWC 64840) off the Edwards Plateau in Tamaulipan desert vegetation establishes the existence of a narrow zone of sympatry between *M. t. girardi* and *M. s. schotti.* The locality is about 38 km southwest of the nearest *M. t. girardi* locality and approximately 33 km northwest of the nearest *M. s. schotti* locality. A hybrid specimen (TCWC 49204) is known from a locality 20 km to the east. Increases in ventral counts in *M. s. ruthveni* and decreases in maxillary tooth and ventral counts of *M. t. taeniatus* away from the contact zone may indicate character displacement (Mayr, 1970). Discordant patterns of character state distributions are found in intermediate specimens from this area, indicating that they may be interspecific hybrids (Lawson and Lieb, 1990). Evidence suggests that the southern Balcones Escarpment may be a narrow hybrid zone (sensu Moore, 1977).

Two additional contact zones may exist between *M. taeniatus* and *M. schotti.* The first of these is the previously mentioned area of northeastern Mexico, where four putative hybrids were found. However, this is problematical, because no specimens of *M. t. girardi* are known as yet from near this locality. The second is a *M. t. girardi* (CAS 165260) from northeastern Jalisco which is sandwiched in an area of parapatry between the ranges of *M. s. ruthveni* and *M. bilineatus,* suggesting a potential contact zone involving all three species.

Despite character state similarities among these three species, and areas of sympatry involving *M. taeniatus* and *M. bilineatus,* no hybrids involving the latter species were found. *Masticophis bilineatus* differs from the other two species in having the plesiomorphic character state of 17 dorsal scale rows. *Masticophis taeniatus* and *M. schotti* are shown to be sister species on the basis of the synapomorphic condition of 15 dorsal scale rows. Little intraspecific variation in anterior and midbody dorsal scale rows are known for any *Masticophis.* Thus, *M. bilineatus* is considered the most divergent of the three species examined.

Southward decreases in ventrals of *M. bilineatus* (Fig. 4, 5) as found in this study were also reported by Ortenburger (1928). Ventral variation among samples 18–21 indicates a step cline, whereas subcaudal variation is more gradual (Fig. 4–7). Differences between snake populations inhabiting Sonora and Sinaloa were discussed for *M. flagellum* (Wilson, 1970) and *Hypsiglena* (Dixon and Dean, 1986). The latter authors identified a hybrid zone in the foothills along the Río Fuerte in northern Sinaloa that is a transition area from lower Sonoran Desert vegetation to tropical thorn scrub. Two male *M. bilineatus* from the lowlands along the Río Fuerte agree with northern (Sonoran Desert) specimens in ventral number. Perhaps the contact zone between the low and high ventral count forms is farther east in the foothills, as in *Hypsiglena,* or immediately to the south of the Río Fuerte. However, no specimens of *M. bilineatus* and *Hypsiglena* are available from between Los Mochis and Guamuchil, Sinaloa (Dixon and Dean, 1986). The southern low-ventral form of *M. bilineatus* may constitute a separate subspecies (C. H. Lowe, personal communication). However, multivariate analyses did not separate these samples (Fig. 8, 9) and *Masticophis bilineatus* is therefore considered monotypic.

Genetic differentiation is low among the taxa examined here. Since other snake species are known to show low levels of genic differentiation (Gartside et al., 1977; Murphy and Ottley, 1980; Murphy, 1983; Murphy and Crabtree, 1985; Lawson, 1987; Lawson and Lieb, 1990), this is not indicative of measurable gene flow. Murphy (1983) reported Nei's genetic identity values of 0.89 between *Masticophis lateralis* and *M. aurigulus,* and 0.94 between *Crotalus ruber* and *C. catalinensis.* Speciation with little genic differentiation is well-known among many taxa (see citations in Gartside et al., 1977). They reported Rogers' S values of 0.91–0.94 with little morphological differentiation between the ribbon snakes, *Thamnophis proximus* and *T. sauritus.* Rogers' S values among the morphologically better-differentiated *M. taeniatus* and *M. schotti* range from 0.93–0.97. Degree of genic differentiation is more closely associated with time since divergence (Avise and Ayala, 1976). Differentiation of *M. schotti* and *M. taeniatus* may have resulted from a Recent speciation event, possibly divergence in allopatry during habitat changes brought about by Wisconsin glaciation, with secondary contact occurring presently along the Balcones Escarpment. Populations of whipsnakes now known as *M. taeniatus* may have been isolated in the Chihuahuan Desert refugia of north-central Mexico, while the ancestors of *M. schotti* were restricted to the Tamaulipan grassland refugium of eastern Mexico (Morafka, 1977). However, because *M. taeniatus* and *M. schotti* are sister species, one cannot distinguish between a primary and secondary origin for the Balcones Escarpment contact zone (Wiley, 1981).

The existence of the *A* allele of the *S-Aat-A* locus in one specimen of *M. s. ruthveni* from extreme southern Texas is problematical. Three possibilities exist. First, the presence of this allele in *M. schotti* may be the result of introgression from *M. t. girardi* in Mexico. This may occur at one of the two potential contact zones previously mentioned. With the apparent absence of *M. t. girardi* near the potential contact zone in northern Mexico, and a lack of intermediate specimens from the south-central Mexican plateau area, little evidence in support of this hypothesis exists. Second, the observed pattern of geographic variation in alleles at this locus may be a function of small sample size, with all alleles being present in both species. It has been shown that sample sizes as small as those used here are adequate for estimating genetic divergence (Nei, 1978; Gorman and Renzi, 1979). However, answering this question necessitates a population genetics approach and not simply a measure of genetic divergence. Even though sample sizes are insufficient for population genetic studies of these species, the fixed difference across the Balcones Escarpment contact zone appears real. Evidence for this hypothesis lies in the step clinal pattern of variation of several morphological characters and the paucity of specimens with intermediate phenotypes or genotypes. Finally, the *A* allele of the *S-Aat-A* locus may be a residual allele common to the ancestor of *M. schotti* and *M. taeniatus* such as that hypothesized for *Anguilla* by Avise et al. (1990). It appears that there is character state divergence at the *S-Aat-A* locus with respect to the Balcones Escarpment contact zone, with the *A* allele not yet extinct in *M. schotti* populations located away from the contact zone. Since *M. schotti* is variable at this locus, with the *A* allele still present, Recent divergence with differential selection pressures within each of these two species is suspected. The last hypothesis is preferred, since it is most concordant with the more conclusive morphological data set. However, more specimens from throughout the ranges of both species must be assayed for genetic variation in order to fully test these hypotheses.

Although we have not previously discussed the relationship of *Masticophis* to other related genera, for example *Coluber, Mastigodryas, Dendrophidion,* and possibly *Drymobius,* at this time we do not propose the synonymy of *Masticophis* and *Coluber.* It is obvious to us that the latter genera may well be congeneric, as suggested by Schätti (1986, 1987) and Stejneger and Barbour (1917). We suspect that *Masticophis* sensu stricto is not a valid genus because of the evidence from osteology and hemipenis morphology presented by Schätti (1986, 1987).

ACKNOWLEDGMENTS

We would like to thank the following for live specimens or tissue samples: R. Baker, B. Buchanan, J. Campbell, L. Densmore, C. Farquhar, R. Green, C. Harrison, R. Jennings, J. Johnson, B. Keeley, K. King, W. Lamar, T. Lee, C. Lieb, R. Macken, R. Martin, H. McCrystal, P. Mckeown, A. Price, A. Rentfro, N. Scott, R. Wallace, R. Worthington, and the Texas Herpetological Society. Special thanks go to R. and B. Houston, who graciously gave us access to their land in Llano County, Texas. Marc Allard, G. Baumgardner, H. Camper, J. Derr, I. Greenbaum, H. Greene, B. Hanks, M. Morris, A. Price, M. Retzer, K. Reed, M. Sims, S. Smith, and P. Sudman provided help during data collection or analysis. We thank the following institutions (and curators) for loans of specimens: American Museum of Natural History (AMNH, C. Myers, R. Zweifel), Academy of Natural Sciences, Philadelphia (ANSP, J. Cadle, E. Malnate), Angelo State University (ASC, M. Engstrom), Arizona State University (ASU, M. Douglas), Baylor University–Strecker Museum (SM, D. Lintz), Brigham Young University (BYU, J. Sites), Chicago Academy of Sciences (CA, R. Vasile), California Academy of Sciences (CAS, R. Drewes, J. Vindum), Carnegie Museum of Natural History, Pittsburgh (CM, E. Censky, C. J. McCoy), Cornell University (CU, K. Adler, R. Schoknecht), Dallas Museum of Natural History (DMNH, K. Krumke), Drake University (DURC, J. Christiansen), Ernest A. Liner (EAL), Field Museum of Natural History, Chicago (FMNH, H. Marx), Fort Worth Museum of Science and History (FWM, W. Voss), Illinois Natural History Survey (INHS, K. Cummings, L. Page, M. Retzer), University of Kansas Museum of Natural History (KU, J. Collins, W. Duellman), Los Angeles County Museum (LACM, R. Bezy, J. Wright), Harvard University–Museum of Comparative Zoology (MCZ, P. Alberch, J. Rosado), Kerr Wildlife Management Area, Kerrville, Texas (KWMA), Louisiana State University–Museum of Zoology (LSUMZ, D. Rossman), Midwestern State University (MU, F. Stangl), National Museum of Natural History (USNM), R. McDiarmid, R. Reynolds, G. Zug), New Mexico State University (NMSU, J. Lapointe), San Diego Natural History Museum (SDNHM, G. Pregill), Southern Illinois University (SIUC, R. Brandon, M. Morris), Southwestern Research Station, Portal, Arizona (SWRS, W. Sherbrooke), Staatliches Museum für Tierkunde (MTKD, F. Obst), Sul Ross State University (SRSU, J. Scudday), Texas A&I University (TAIC, A. Chaney, S. Smith), Texas A&M University–Texas Cooperative Wildlife Collections (TCWC, M. Retzer, K. Friend), Texas Tech University Museum (TTU, C. Jones), Tulane University (TU, H. Dundee), University of Arizona (UAZ, G. Bradley, C. Lowe), University of California at Berkeley–Museum of Vertebrate Zoology (MVZ, D. Good, H. Greene), University of Florida–Florida State Museum (FSM, D. Auth), University of Idaho–Museum of Natural History (UIM, R. Wallace), University of Illinois–Museum of Natural History (UIMNH, L. Maxson), University of Michigan Museum of Zoology (UMMZ, A. Kluge), University of New Mexico–Museum of Southwestern Biology (UNM, H. Snell), University of Northern Arizona–Museum of Northern Arizona (MNA, D. Howard), University of Oklahoma–Stovall Museum (UO, J. Krupa), University of Southwestern Louisiana (USL, J. Jackson), University of Texas–Texas Memorial Museum (TNHC, R. Martin), University of Texas at Arlington (UTACV, J. Campbell, J. Darling), University of Texas at El Paso (UTEP, C. Lieb), University of Utah (UU). In particular, we would like to thank J. V. Vindum (CAS) for calling our attention to four recently accessioned specimens from Mexico in his care. We thank José Luis Villarreal B. for translating the abstract. This research was funded by the Texas Agricultural Experiment Station and a Texas A&M University Faculty-Staff minigrant.

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APPENDIX 1

Specimens Examined

(See Acknowledgments for explanation of museum abbreviations)

Masticophis taeniatus.—**UNITED STATES: ARIZONA:** *Apache Co.,* Chinle (MCZ 8972), Concho (SDNHM 44192), 1 mi S Hat (UNM 11976), Petrified Forest National Park (UTACV 14342), 2 mi N Springerville (BYU 16673), 4 mi E St. Johns (MVZ 9327), 4 mi S St. Johns (UAZ 39492), 11 mi S jct US 666 & AZ 61 (UAZ 27270); *Cochise Co.,* 8 mi S. Willcox (NMSU 1965); *Coconino Co.,* no locality (FMNH 25721, UAZ 25726), Bright Angel Canyon (UAZ 25716–25717), Buckfarm Canyon (MNA Z7.2405), Coal Mine Canyon (CA 15905), Glen Canyon (UAZ 39719), Grand Canyon (AMNH 63857, 97792, MNA Z7.2827, SDNHM 3158–3159, USNM 50953, 239259–239260), 22 mi S Cameron (MVZ 25484), Coleman Lake (MVZ 29083), 13 mi N Deadman's Flat (MZ 8680), 11 mi E Desert View (UAZ 34753), Flagstaff (LACM 27773), 17 mi ENE Flagstaff (MNA Z7.624), 28 mi N Flagstaff (BYU 22113), 3 mi N Fredonia (UAZ 25723), 5.7 mi S Fredonia (UAZ 25731), 14 mi E Jacob Lake (CA 10123), 42 mi SW Kayenta (CM 66657), Oak Creek (CAS 35235), Rainbow Lodge (MVZ 17885), San Francisco Mtns (MNA Z1.44), 15 mi E Seligman (LACM 20592), 10 mi N Sunset Crater National Monument (UTEP 4123), 15 mi N The Gap (SM 3961), 12 mi SE Tuba City (CAS 156190), 19 mi SE Tuba City (AMNH 114528), 24.7 mi SE Tuba City (UAZ 25720), Two Guns (SDNHM 32324), Wupatki National Monument (INHS 6500, LACM 20591, MNA Z7.5, Z7.656), 2.6 mi N US 89 on alt US 89 (UAZ 25730); *Gila Co.*, no locality (USL 8946), Crook National Forest (UIMNH 72093), 11 mi N Miami (FMNH 106182–106283), Pine (BYU 11291), 3 mi NW Pine (CA 17900), Pioneer Peak S of Globe (UIMNH 72092), Pinal Mtns (UAZ 25722), 8 mi W Roosevelt (UAZ 25725), Roosevelt Reservoir (USNM 105228), 4.3 mi S Rose Creek Campgrounds (UIMNH 72094), Rose Creek Lodge (MVZ 49918), near San Carlos (CM 26675), Sierra Ancha Experimental Forest-SAEF (CM 53796), SAEF T4.5N R21E Sec 31 (ASU 10534–10535), 7 mi SE SAEF Headquarters (ASU 11299), Carris Ranch in SAEF (MVZ 6309), Tick Flat (ASU 10533), 6.8 mi N Young (UAZ 35973); *Graham Co.*, Graham Mtns (USNM 51764), 7.5 mi E Klondyke (AMNH 111226), San Carlos Indian Reservation (CAS 158216–158217), Santa Teresa Mtns (SDNHM 62706); *Greenlee Co.*, Blue Mtns (UNM 22319–22320), 40 mi NW Clifton (UAZ 25724), 7 mi SW New Mexico state line on AZ 78 (UNM 33141); *Mohave Co.*, Cerbat Mtns (UAZ 40571), 7.6 mi E Hackberry (MVZ 170750), 16.3 mi S & 9.5 mi E Hackberry (UAZ 25734), Hualpai Mtn Park (TCWC 9341), 32 mi E Kingman (MVZ 175138), 35 mi W Kingman (TCWC 9340), Mt Trumbull (UAZ 25719), 11.8 mi E jct US 40 & AZ 93 on US 40 (LACM 135203), 8.2 mi W jct Main St Valley Rd & Virgin Mtn Rd (UAZ 25715), 15.1 mi E jct Main St Valley Rd & Navajo Trail (UAZ 25718), 13.5 mi E Yucca (MNA Z7.656); *Navajo Co.*, 12 mi W Cibecue (MCZ 101217), New Orabi (AMNH 110454, UAZ 25727), Paiute Canyon (MVZ 17884), S of Taylor (BYU 13599); *Pinal Co.*, SE Superior (UIMNH 72095); *Yavapai Co.*, Bradshaw Mtns (AMNH 63978), 9.8 mi NW Congress (UIMNH 71995), Cottonwood (ASU 208223, CM 66655, FMNH 208223), 4 mi SW Cottonwood (CM 66656), Granite Dells (UAZ 9333–9334), 3 mi W Iron Springs (UAZ 25732), Milk Creek (UAZ 25728), Mingus Mtn (CM 66660), 1 mi N Montezuma's Castle National Monument (EAL 3084), Peeples Valley (UIMNH 72096), Prescott (ASU 1614, UAZ 25729, USNM 15704), 12 mi SW Prescott (AMNH 126735), 13.6 mi NNE Prescott (CM 66659), 4 mi W Sedona (UIMNH 43200), 7 mi W Sedona (CM 66661), Whipple (MCZ 5865, USNM 11422–11423), Yarnell (CA 3151, SDNHM 32325), 1 mi S Yarnell (SDNHM 5290), 6 mi N Yarnell (CA 3468); *Yuma Co.*, 3 mi S & 6.2 mi W Gladden (UAZ 25735), Kofa Mtns (UNM 41621, USNM 221843–221844). **CALIFORNIA:** *Alameda Co.*, near Oakland (CAS 10639); *Inyo Co.*, Argus Mtns (SDNHM 17061), 18 mi N Cowhorn Valley (SDNHM 48083), 5 mi W & 1.25 mi S Independence (MVZ 38410–38411), 6 mi W Independence (AMNH 110680); Panamint Mtns (MVZ 19256, 64131); *Lassen Co.*, 9 mi E Amedee (MVZ 24579), Bare Creek Ranch (LSUMZ 8802–8803), Fort Sage Mtn (MVZ 20481), Lassen National Park (MVZ 68313), 5 mi E Litchfield (MVZ 36136), 6 mi E Susanville (UMMZ 91821); *Modoc Co.*, 6 mi N Eagleville (LSUMZ 8804); *Mono Co.*, 2 mi S Benton (MVZ 3714), between Hot Creek & Mammoth Jct (CAS 8395), near Hot Creek geysers (SDNHM 19357–19360), Sierra Nevadas (LACM 2270), Topas Lake (SDNHM 28860), Whitmore Tubs (SDNHM 34240); *San Bernardino Co.*, Chemehuevi Mtns (LACM 2272–2274), Clark Mtn (MVZ 28564–28566, 41703), 11.2 km S Lima (MVZ 100271), Midhills Campground (MVZ 150189); *Siskiyou Co.*, Ash Creek at Klamath River (UNM 26436), 3 mi S & 1 mi E Capco (MVZ 85073), Gazelle (CAS 36063), 15 mi NE Weed (MVZ 17259). **COLORADO:** *Garfield Co.*, 6 mi N Mesa Co line (UIMNH 80484), 7 mi W Rifle (USNM 40197); *Mesa Co.*, Colorado National Monument-CNM (CM 42791–42792, 43537, SM 13299), Debeque Canyon (CM 43538), Fruita Entrance to CNM (UIMNH 53217), Grand Junction (FMNH 920), Palisade (USNM 29610), Plateau Creek (USNM 40196); *Moffat Co.*, Jct Green & Yampa rivers (UIMNH 64659); *Montezuma Co.*, 6 mi S Cortez (BYU 41686), Mesa Verde National Park (KU 106150–106151, 129712–129714); *Montrose Co.*, Paradox Valley (SDNHM 8680). **IDAHO:** *Ada Co.*, Boise (CAS 41362–41363, KU 8443, UMMZ 63990–63993), Cinder Cone Butte (CAS 64203–64206, FMNH 6963), Snake River SE Melba (SDNHM 1432), Swan Falls near Snake River (TCWC 64836–64837), near Swan Falls (UIM 329 [6]); *Bannock Co.*, Pocatello (KU 6468, 11803); *Bingham Co.*, no locality (MVZ 28765); *Butte Co.*, Arco (BYU 30771); *Cassia Co.*, Albion (UMMZ 71466), Raft River Valley (BYU 42032); *Elmore Co.*, Cleft (CAS 64185, 64207), 4 mi W Hammett (MVZ 21562), 14 mi S Mtn Home (UIM 196); *Fremont Co.*, Yellow Stone (USNM 56018); *Gooding Co.*, 2 mi S Hagerman (MVZ 18302), between Snake River & Bliss (CAS 4065); *Jerome Co.*, Jerome (TCWC 57856); *Owyhee Co.*, 9.8 mi E Bruneau (UMMZ 133006, 133398), W of Homedale (UMMZ 68299), E of Hot Springs & S of Bruneau (SDNHM 1431), Fossil Butte (UIM 390 [2]), 18 mi SW Nampa (BYU 40813), 22 mi N Nevada State Line (MVZ 24580–24581), lower Reynolds (UIM 291 [2]), Squaw Creek (UIM 103), Sucker Creek (CM 91569), Warm Springs Ferry (CAS 55246); *Twin Falls Co.,* SW 0.25 Sec 28 T17S R13E (UMMZ 125687). **NEVADA:** *Churchill Co.,* 90 mi E Fallon (BYU 16650), 8.5 mi SE Hausen (MVZ 21511); *Clark Co.,* 20 mi SW Indian Springs (UNM 4802), 1 mi N Lee Canyon Rd to Charles Mtns (LACM 59025), 10 mi W Hwy 95 on NV 156 (MVZ 182611), Spring Mtns (CAS 2003); *Douglas Co.,* 3 mi NE Topaz Lake (MVZ 18635); *Elko Co.,* Carlin (UMMZ 43123–43127, 43156, 149867–149869), 15 mi W Wendover, UT (CAS 10025); *Esmeralda Co.,* 12 mi E Oasis (KU 82339); *Eureka Co.,* Dunphy (SDNHM 27787, 27851); *Humboldt Co.,* 10 mi SW Denio (KU 109967), 6 mi S Golconda (MVZ 20622), Pine River Mtn (MVZ 1514, 1516), Quinn River Crossing (MVZ 1513, 1515), 5 mi S Quinn River Crossing (MVZ 21515), 2.5 mi N Ryepatch pump station valley (UMMZ 78026), Valmy (SDNHM 27788), 2 mi W Winnemucca (CAS 120818), 10.2 mi SW Winnemucca (UIMNH 4396); *Lander Co.,* Antelope Spring (USNM 8120), 3 mi E Austin (TNHC 7441), 16.5 mi S Battle Mtn (USNM 218839), 19.3 mi SSE Battle Mtn (USNM 218838), Kingston Creek (MVZ 12171), Toquime Range (MVZ 42085), Toiyabe Range (MVZ 42084); *Lincoln Co.,* Caliente (CAS 36976), 0.5 mi E Panaca (MVZ 56917), 13 mi NNW Pioche (MVZ 61816), N end Timpahute (MVZ 14283); *Mineral Co.,* Excelsior Mtns (MVZ 10865), 18 mi SE Hawthorne (SDNHM 37702), 15 mi ENE Luning (UMMZ 124602); *Nye Co.,* Cloverdale (USNM 44525), 2 mi E Garrett Ranch (SDNHM 40654), Mercury (BYU 17409, 18755–18756), Nevada Test Site (MVZ 140912), N Twin River (MVZ 12843, 16180), 0.5 mi S Oak Spring (MVZ 13082), Rainer Mesa (BYU 23858, 30547), Toiyabe Range (UNM 52432), 0.5 E Tonopah (UNM 463), 18 mi E Tonopah (SM 3962), 24.4 mi ENE Tonopah (CAS 21320), S Twin River (MVZ 12170), White River Valley (UMMZ 86127), Wisconsin Creek (MVZ 12841–12842); *Ormsby Co.,* Carson City (CAS 6527, SDNHM 27785, USNM 9520), 4 mi SW Carson City (MVZ 20395); *Pershing Co.,* Humboldt Range (MVZ 21513–21515), Imlay (MVZ 43150), 5 mi E Lovelock (MVZ 11983), 15.3 mi NW Lovelock (SDNHM 37791); *Washoe Co.,* Little High Rock Canyon (MVZ 7546), 6 mi S Pahrum (MVZ 24582), Pyramid Lake (CAS 6526, 40505, 44146–44147, USNM 44536, 50801), 0.5 mi S Pyramid Lake (MVZ 32100), near Reno (KU 6667), 12 mi NNW Reno (CAS 93781–93784), Smoke Creek 1 mi from CA state line (MVZ 20482), Sutcliffe (CAS 22188); *White Pine Co.,* Baker (CAS 14372), 1.7 mi E El Dorado (MVZ 70341), Major Woods (CAS 14371), Mt. Moriah (MVZ 24583), Spring Valley (UMMZ 84911), 8 mi N Yelland's Ranch (SDNHM 19704). **NEW MEXICO:** *Bernalillo Co.,* 3 mi S Alameda (UNM 18254), Albuquerque (KU 5536, UNM 460, 4722, 11407, 12254, 22551, 22562, 33751, 38812), 17 mi E Albuquerque (AMNH 115716), Hwy 10 10.6 mi S US 66 (UNM 32384), Sandia Mtns (UNM 11611, 15600, 18253, 25658); *Catron Co.,* 10 mi N Alma (UNM 33122), 4 mi W Baldy Creek (NMSU 2956–2957), Glenwood Fish Hatchery (NMSU 3734, 4401), 0.9 mi NE Glenwood (AMNH 120697), 1 mi S Glenwood (UNM 4723), 1.3 mi N Glenwood (CM 48768), 2.5 mi N Glenwood (BYU 13979), 4 mi S Glenwood (UNM 18740), 5 mi S Glenwood (KU 6477–6478), 6 mi S Glenwood (AMNH 114035), 6.5 mi S & 0.5 mi W Glenwood (TCWC 65001), 13.5 mi E Glenwood (UNM 11535), 1 mi W Mogollon (UTEP 1711), Nichols Canyon (NMSU 5328), Pleasanton (UNM 32169), 4 mi S Pleasanton (UTEP 1710), San Francisco Hot Springs (UAZ 25714, UNM 38853), Whitewater Canyon (UNM 6794); *Chaves Co.,* Bishops Cap (UTEP 2540), Elk (LACM 20598), Jornada Experimental Range (USNM 102252), 4 mi N Las Cruces (LACM 133881), 8 mi N Las Cruces (LACM 2279), 11 mi S Las Cruces (DMNH 1930), 11 mi N Las Cruces (LSUMZ 10027), 12 mi N Las Cruces (LACM 2278), 22 mi W & 15 mi N Las Cruces (LACM 133882), 14.9 mi E Mayfield (LACM 20597), 2 mi W & 1 mi S Mesilla (LACM 133883), 5 mi S Mesilla (UTEP 107), Organ Mtns (UTEP 9509), 3.9 mi N Organ (LACM 103360), Picacho Canyon (NMSU 2833), 1 mi S Radium Springs (CU 5056), 1 mi N Radium Springs (NMSU 1984), 1 mi E Rincon (UTEP 7639), 13 mi N & 4.6 mi E University Park (KU 72916), 3.2 mi S US 70 on Aguirre Springs Rd (NMSU 5837); *Eddy Co.,* no locality (UTEP 7660), 30 mi SW Carlsbad (CM 18297), NM 137 W Carlsbad (UNM 37796), Carlsbad Caverns National Park (TTU 3581, UMMZ 121794, 121797–121798, 123477, 125338, UNM 30458, 30926), Dog Canyon Rd 4 mi N TX state line (TTU 9679), Guadelupe Mtns (UMMZ 123470, UNM 25729), Rattlesnake Canyon (KU 8386), Robinson Draw (UMMZ 123473), 1 mi N Whites City (UMMZ 121795–121796); *Grant Co.,* Blue Creek (NMSU 5259), 5 mi NW Buckhorn (UNM 6425), Gertie Canyon in Big Burro Mtns (MVZ 7119), Burro Mtns (NMSU 4694, UTEP 1974–1975), 4 mi S Cliff (NMSU 4391), 4 mi N Cliff (NMSU 3733), 5.5 km E & 6.2 km N Cliff (UNM 37768), 7.5 mi N Cliff (NMSU 4395), 10.5 mi N Cliff (UAZ 35078), 16 mi SW Cliff (NMSU 4392), 16 mi S Cliff (NMSU 4396), City of Rocks State Park (KU 72917), Dwyer (KU 109968), Gila National Forest (UNM 38913), Gila River (NMSU 6019, UNM 461), Hachita (AMNH 85071), 18 mi N Lordsburg (UIMNH 72091), N of Mimbres (CA 5312), 1 mi N Mimbres (UNM 32862, UTEP 7638), 5 mi N Mimbres (UMMZ 79215), Mimbres River Valley (NMSU 4399), Pinos Altos (UAZ 25713), 2.75 mi NNW Pinos Altos (AMNH 84991), Redrock (NMSU 3730), 5 mi NE San Lorenzo (UTEP 1345), Sapillo Creek Bridge (NMSU 4512), 2 mi W Sapillo Creek Bridge

(NMSU 4390), Sawmill Creek (UNM 38932), Silver City (MVZ 42593, NMSU 4397, 4513, 4696–4697), 1 mi S Silver City (UNM 4721), 2.9 mi W Silver City (UTACV 2621), 3 mi S Silver City (NMSU 4493), 10 mi S & 8 mi W Silver City (UNM 15205), 13 mi W Silver City (UNM 15294), 19 mi W Silver City (NMSU 4695), 20 mi S Silver City (TCWC 63047), 25 mi SW Silver City (NMSU 4400), Slades Canyon (NMSU 4394), 1 mi NNE Vanadium (NMSU 4389), 10.7 mi NNE White Signal (UTEP 8763), jct NM 61 & Hwy 90 (LACM 76408), Sec 12 T18S R16W (NMSU 4398), 13.3 mi NE jct NM 90 & US 70 (UNM 32033); *Hidalgo Co.,* Alamo Hueco Mtns (AMNH 78996, UTEP 11355), 4.5 mi NW Antelope Wells (NMSU 1868), 39 mi S Hatchita (ASC 10952), 0.7 mi S Grant Co line (UNM 6793), Little Hatchet Mtns (AMNH 74725, 75410, UTEP 10570), 1.8 mi W jct NM 530 & 92 (NMSU 5347); *Lincoln Co.,* Corona (LACM 2277), 2 mi NW Carrizozo (UMMZ 67658), 4 mi NW Carrizozo (AMNH 111227), 2 mi NW Hondo (UNM 23558), Tularosa Malpaise (UNM 37153), 0.5 mi N White Oaks (UNM 31673); *Luna Co.,* 5.7 mi N Columbus (LACM 103361), 21.5 mi W Columbus (TCWC 56339), 19 mi NNE Deming (UTEP 5676), 10 mi NW Florida (NMSU 4514), Florida Mtns (UTEP 200, 11261), 2 mi N Nutt (LACM 109526), Tres Hermanas Mtns (UNM 462); *McKinley Co.,* 5.9 mi N Ya-ta-hey (UTEP 9540); *Otero Co.,* Alamo Mtn NW 0.25 Sec 21 T26S R13E (NMSU 6329), 1 mi NE Alamogordo (NMSU 4698), Dog Canyon (USL 24962), 7.5 mi E LaLuz (LACM 20599), SW 0.25 Sec 33 T17S R10E (NMSU 6186–6187); *Quay Co.,* 9 mi W & 1.5 mi S Tucumari Mtn (UNM 19705); *Rio Arriba Co.,* 14 mi NW Abiqui (UAZ 39721), Nutria (USNM 8432); *Sandoval Co.,* 4 mi S Algdones (UNM 16697), Bandelier National Monument (UNM 30534), 15.2 mi SE Cuba (UNM 22071), Jemez Mtns (UNM 30879), Jemez Pueblo (UNM 459, 4720), Juan Tabo Picnic Area (UNM 10902, 13518, 37797), Placitas (UNM 458, 18255), 2 mi SW Placitas (CM 58692), Sante Fe National Forest (UTEP 8926); *San Juan Co.,* Chaco Canyon National Monument (UNM 3395, 21835–21839), 2.6 mi S Newcomb (UAZ 36364), Shiprock (USNM 2110 holotype, 44503), 4 mi W Shiprock (UTACV 1182), NE 0.25 Sec 24 T32N R7W (UNM 4153), Wool Canyon (UU 3738); *San Miguel Co.,* 1 mi below Conchas dam (UNM 21909), 3 mi below Conchas dam (UNM 18256), 1 mi N Sena (UNM 32863), 7.3 mi SE Trujillo (LACM 20600); *Santa Fe Co.,* 4 mi N Golden (UNM 31669), Jemez Mtns (UNM 364643), 5 mi NE Los Cerillos (UNM 456), 1.5 mi S Madrid (UNM 23514), 2 mi N Madrid (UNM 10243); *Sierra Co.,* Arrey (NMSU 1477), Caballo Dam (UTEP 152), Elephant Butte (LACM 2276), 2 mi N Ft McCrae (NMSU uncatalogued), Hillsboro (UAZ 40319), 0.8 mi W Hillsboro (UTEP 10698), 3 mi W Hillsboro (NMSU 2028), 3 mi S Hillsboro (LACM 76409), 16 mi E Hillsboro (LACM 76417), Hospital Canyon (NMSU 5531), 2 mi N Lake Valley (NMSU 4402), 1 mi N Truth or Consequences (LACM 2275), 3 mi W Truth or Consequences (NMSU 2020), 12 mi N Truth or Consequences (UNM 13730), 1.5 mi W jct NM 52 & 135 on 135 (NMSU 5484); *Socorro Co.,* 2.3 mi E Bingham (UNM 12762), 6 mi E Bingham (LACM 20594), 12 mi SE New Bingham (LACM 20596), Chupadera Mesa (LACM 63453), 15 mi W Corrizozo (UNM 16745), 3 mi E & 3 mi S Dusty (TCWC 66165), 13.5 mi NE Magdalena (UNM 30880, 30895), Magdalena Mtns (UNM 4154–4155, 13855), Mockingbird Gap (LACM 20595), Rio Salado (UNM 14876), 8.9 km W & 1.4 km N I-40 bridge over Rio Salado (UNM 39258), 15 mi S & 3 mi E Rosedale (KU 47791), 25 mi SW San Antonio (UNM 455), 8.7 mi W Socorro (LACM 20593), 16.1 mi W Socorro (UNM 11525); *Torrance Co.,* 9 mi W Mountainair (UNM 457); *Valencia Co.,* 9 mi N Acoma (MVZ 128112), 5 mi E Grants (CU 3052), 6 mi NE Grants (UNM 22332), 8 mi E Grants (UNM 8843), 10.4 mi S Grants (CU 5602), Mesa Encantada (UNM 30896). **OREGON:** *Crook Co.,* no locality (MVZ 26924); *Deschutes Co.,* 3 mi W Terrebonne (UNM 33169), 4 mi W Terrebonne (UNM 30941); *Harney Co.,* Fields (UMMZ 133342, 133379), 3 mi S Fields (UMMZ 133091), 6 mi S Fields (UMMZ 133001, 133092 [3]), Frenchglen (CM 20745); *Lake Co.,* Picture Pass Summit (UMMZ 135986); *Malheur Co.,* 5 mi S Adrian (UMMZ 124574); *Wasco Co.,* Maupin (MVZ 62055); **TEXAS:** *Bandera Co.,* 18 mi NW Medina (TNHC 1904), 6 mi S Tarpley (SM 7491), 13 mi W Tarpley (UNM 37798); *Bexar Co.,* Helotes (SM 228–229), 1 mi N Helotes (MVZ 68462), Helotes Creek (CU 609, SM 6384), San Antonio (UNM 13522, UTEP 9595), 17 mi N San Antonio (AMNH 22743, 74548), 18 mi N San Antonio (CM 22850), 22 mi N San Antonio (CU 1771–1772); *Blanco Co.,* 4.9 mi W Johnson City (USL 1793), 5.7 mi E Johnson City (USL 1792), 17 mi SE Johnson City (TNHC 28913), 20 mi NW Johnson City (MCZ 62561), 16.9 mi E Sandy (LSUMZ 14149); *Brewster Co.,* no locality (SRSU 1469, UMMZ 71925), Alpine (CAS 7503, SRSU 1844, 4587), 10 mi S Alpine (SRSU 1694), 22 mi S Alpine (TCWC 28940), 42 km S Alpine (KU 176790), 32.1 mi S Alpine (LSUMZ 23342), 59.5 mi S Alpine (USL 6799), 65 mi S Alpine (SRSU 1845), Big Bend National Park (AMNH 72527, 77318, 111228, CA 7821, CM 5006, 60005, FMNH 26617–26618, 26803–26804, 27707–27708, 27845, LACM 103362–103363, MVZ 25362, SM 6388-6392, SRSU 3927, 5079, TCWC 16127–16128, 40111, TTU 4, 629, UAZ 34784, 39228, 40391, UMMZ 66026–66029, 72088, 95435, UNM 9025–9026, 18258, 20801, 20891–20893, 22238, 22381, USNM 103638, UTACV 2619), 1 mi N BBNP on Hwy 118 (UMMZ 32386), 13 mi N BBNP on Hwy 118 (UIMNH 47645), Black Gap Wildlife Management Area (DMNH 296, 302, TCWC 12296, TNHC 12603, 12797, 12984), Boquillas (CA 4860), Lajitas (KU 51945), Marathon (SM 5926–5927), 12 mi S Marathon (UMMZ 20827), 12 mi S & 2 mi W Marathon (FWM

6910), 13 mi S Marathon (SRSU 4665), 22 mi E Marathon (MVZ 53916), 31 mi SE Marathon (SRSU 1671), Reed Plateau (TCWC 64999), Rosillos Mtns (FMNH 75480–75482, UMMZ 114344), 25 mi W Sanderson (AMNH 94276), Santiago Mtns (UMMZ 114203), Study Butte (NMSU 3210), 7 mi W Study Butte (NMSU 3211), 10 mi S Study Butte (SRSU 2193), 28.5 km N Study Butte (UTACV 12736), Terlingua Ranch (TCWC 65285), 1.1 mi W jct Hwys 170 & 118 on 170 (TCWC 63376), 4 mi N jct Hwys 118 & 170 on 118 (UTEP 10569), 48.9 mi S jct Hwys 118 & 90 on 118 (TCWC 63378); *Burnet Co.,* Clear Creek (CAS 33072, SM 752), 12 mi W Inks Dam (TNHC 2639), 7 mi NW Marble Falls (TAIC 1414); *Coleman Co.,* 0.25 mi N Santa Anna (UTACV 2620); *Comal Co.,* 1 mi NW Fischer (TCWC 25397), Hunter (UMMZ 74328), New Braunfels (UMMZ 69662), 3.5 mi NNE New Braunfels (MVZ 99224), 5 mi NW New Braunfels (UMMZ 74074); *Concho Co.,* 50 mi SE San Angelo (LACM 74105); *Crockett Co.,* Howard Springs (USNM 1970), 17 mi E Iraan (TCWC 40112), 15 mi W Ozona (UAZ 25757), jct Pecos River & Independence Creek (TU 14472); *Culberson Co.,* Guadelupe Mtns National Park (SM 4881–4882, TCWC 65904, TTU 9675, UMMZ 70134, 123469, 123514, USNM 147878), 6 mi N Kent (MU 4130), 2 mi NE Nickle (KU 72759–72760), Pine Springs (SDNHM 25483), 2 mi W Van Horn (TTU 4741), 15 mi N Van Horn (UMMZ 91474), 25 mi N Van Horn (TCWC 18299–18300); *Edwards Co.,* 0.5 mi W Real Co line on TX 41 (TNHC 44638), 4 mi E Rocksprings (TTU 9715), 7 mi E Rocksprings (UMMZ 102443), 20 mi S Rocksprings (TCWC 65923), 21 mi NE Rocksprings (DMNH 5254), 44.2 km S jct Hwys 290 & I-10 (UTACV 14737); *El Paso Co.,* El Paso (DMNH 2341, 4113, NMSU 5501, UMMZ 74072, UTEP 49, 319–322, 816, 2693, 3368, 3677, 4122, 9073, 10572, 10781, 10804, 11178), Hueco Tanks State Park (UTEP 418, 725, 969, 1043, 1656, 2841, 4369, 10452), 5 mi E Hueco Tanks SP (MVZ 37008); *Gillespie Co.,* 8 mi NE Fredericksburg (TCWC 27390), 10 mi N Fredericksburg (SM 12621), 18 mi N Fredericksburg (TCWC 5204); *Hays Co.,* no locality (ASU 2413), Dripping Springs (TNHC 29046), 4 mi E Dripping Springs (TU 18219), Pollard Wildlife Refuge (TCWC 38792), San Marcos (AMNH 32412), 12 mi WNW San Marcos (SIU-C 226), 15 mi WNW San Marcos (UMMZ 105236), 17 mi NW San Marcos (FSM 56659), Wimberley (FMNH 55049, UTACV 1582), 3 mi S Wimberley (LSUMZ 5852), 7 mi SE Wimberley (TCWC 19030–19031), Wren Ranch Blanco River (FMNH 38061); *Hudspeth Co.,* Eagle Mtns (UTACV 2361, UTEP 1937), 4.5 mi S Hilltop (SRSU 1559), 9.6 mi W Indian Hot Springs (SRSU 4336), Quitman Mtns (UTEP 7455), Sierra Blanca (UTACV 591), 9 mi W Sierra Blanca (KU 40335), 8.2 mi W Van Horn (UTEP 11171); *Jeff Davis Co.,* no locality (NMSU 5838), 14 mi NW Alpine (FSM 56661), 15 mi NW Alpine (SRSU 1846), 29.4 mi NW Alpine (FSM 56660), Davis Mtns (FWM 2530, SM 11532, SRSU 1506, TAIC 4870, TCWC 612, UMMZ 49975–49976, 52925, 81978, UTEP 6812, 10497, 10735), Davis Mtns State Park (AMNH 115717, NMSU 3186, SM 13273), Ft Davis (SRSU 1849–1850, USNM 1971 holotype), 3 mi N Ft Davis (UMMZ 69666), 14 mi N & 8 mi E Ft Davis (KU 56236), 16 mi W Ft Davis (TNHC 7044), 20 mi NW Ft Davis (FSM 56662), 1 mi S Kent (SRSU 1973), 8.5 mi S Kent (UTACV 2701), 3 mi NW McDonald Observatory Rd on 118 (UNM 37799); *Kendall Co.,* Boerne (SM 1901), 11 mi N Boerne (TTU 52), Kendalia (LSUMZ 40055); *Kerr Co.,* 3.6 mi W Hunt (UTACV 2618), 5 mi W Hunt (TCWC 199), 12.9 mi from Hunt (TCWC 47133), 8 mi SW Ingram (TCWC 198), 8.3 mi S & 2.5 mi W Kerrville (TNHC 11933), 10 mi W Kerrville (TCWC 197), 13 mi S Kerrville (TAIC 1058, 1330, 1839, 2618), 17 mi NW Kerrville (TU 14496), 25 mi W Kerrville (UTACV 2194), Kerr Wildlife Management Area (KWMA 1 specimen, TCWC 19033, 25396); *Kimble Co.,* no locality (SRSU 1851), 3.8 mi N Cleo (SM 12620), Crow Ranch (TCWC 65287), Junction (TCWC 64809, 65284), 6 mi W Junction (KU 61061), 10 mi E Junction (MU 3040), 10 mi W Junctin (TNHC 29049), 10 mi NNW Junction (TTU 6048), 12 mi NE Junction (SRSU 1852), 15 mi NW Junction (ASC 8130), US 290 SW corner of county (LACM 66805), 1.5 mi W Telegraph (TAIC 3050); *Llano Co.,* 12.8 km S Cherokee (TCWC 63772–63773, 63876, 64841, 65000, UTACV 11126), Enchanted Rock State Natural Area (AMNH 74547, MVZ 128100, TNHC 4498, 4501, 4503, 29048, TU 13549), S of Llano (TNHC 29045), 2.5 mi W Llano (TNHC 12290), 3 mi W Llano (TCWC 64996), 6 mi SW Llano (UTACV 508), 8 mi E Llano (TCWC 64996), 9 mi N Llano (TCWC 531), 19.2 km NNE Llano (UTACV 14738), 19 mi SW Llano (TCWC 58488–58489); *Mason Co.,* 1 mi E Katemcy (ASC 10549), 2 mi WNW Katemcy (ASC 10813), 3.2 mi WNW Katemcy (ASC 10205), 9 mi SE Mason (ASC 386), 9.1 mi W Mason (TCWC 40110), 10 mi W Mason (TCWC 8734), 12 mi S Mason (TCWC 33797), 12 mi NE Mason (TCWC 3298), 13 mi W Mason (SM 11531), 20 mi ESE Mason (TCWC 31125), Olga Zesch Ranch (TCWC 31126); *McCulloch Co.,* S Brady at San Saba River (FWM 3174), FM 734 at San Saba River (TCWC 19032), 2 mi N San Saba River on Hwy 71 (TCWC 64838); *Medina Co.,* Rio Medina (CM 19919), Hwy 173 at Verde Creek (TCWC 63775); *Menard Co.,* 2.5 E Menard (TCWC 38015), 3 mi E Menard (TCWC 42362), 10 mi W Menard (SM 8951), 10 mi SW Menard (TNHC 12262); *Mills Co.,* 15 mi SSW Goldthwaite (TNHC 14101); *Pecos Co.,* ANSP 15621, 15654, 17076; LACM 66802 15 mi E Ft Stockton; TCWC 27383 13 mi E & 1 mi N Bakersfield; UNM 12079 Huckabee Ranch; *Presidio Co.,* 8 mi NE Candelaria (TCWC 27637, 27639–27643), 9 mi NE Candelaria (TCWC 27639), 24 mi SW Ft Davis (TTU 4290), Kingston Hot Springs (TCWC 64810–64811), 3 mi W Lajitas (AMNH 112229), 12.1 mi W Lajitas (TCWC

65286), 20.2 mi W Lajitas (TCWC 64324), Madera Canyon N Hwy 170 (SRSU 3931), 16 mi S Marfa (TCWC 30516), 63 mi S Marfa (TNHC 14975-14978), 3 mi E Porvenir (FMNH 46037), 15 mi E Porvenir (TNHC 3589), 1 mi SE Presidio (TCWC 27892), 3 mi SE Presidio, (TCWC 27893), 7 mi E Presidio (ASC 10379), 12 mi N Presidio (SRSU 1848), 16.5 mi N Presidio (SRSU 2298), 29.9 mi N Presidio (CM 60598), 7 mi SE Redford (TCWC 27894), 7.3 mi SE Redford (USL 6834), 12.8 mi SE Redford (TCWC 40112), 13 mi SE Redford (SRSU 3561), 13.5 mi SE Redford (TCWC 26171), 17.5 mi SE Redford (LSUMZ 28669), 7 mi N Ruidosa (SRSU 1972), 4.5 mi S Shafter (UTEP 2773), 6.8 mi SW Shafter (LSUMZ 23332), 13 mi N Shafter (DMNH 4227), 19 mi N Shafter (SRSU 4733), 9 mi W jct US 67 & FM 170 on 170 (TCWC 29375), 23.2 mi E jct US 67 & FM 170 on 170 (TCWC 63377), 11 mi W Valentine (TNHC 2851, 3528, 3819, 3837, 3914, 4042, 4262, 15299, 17899); *Reagan Co.*, 9 mi W & 11 mi S Big Lake (ASC 9572), 9 mi S & 12 mi W Big Lake (TCWC 31376); *Real Co.*, 4.5 mi S Leakey (CM 42793), Prade Ranch (FMNH 55018–55019); *Reeves Co.*, Toyahvale (TNHC 1927); *San Saba Co.*, 2 mi W Bend (FWM 5219), 6 mi SE Bend (ASC 385, 5195), 11 mi NW Bend (FWM 5460–5461), 17.5 mi W Lampasas (UTACV 5571), near San Saba (TCWC 20170–20171), 11 mi SW San Saba (FWM 1759–1760), 12.1 mi SE San Saba (FWM 6061), 18 mi NNW San Saba (TNHC 11985–11896); *Sutton Co.*, E of Sonora (LACM 66804), 4 mi S Sonora (KU 82337), 14.9 mi WNW Sonora (UTEP 113); *Terrell Co.*, Chandler Ranch (SRSU 1732, 1971, 1974), 7 mi N Dryden (MU 3897), 8.8 mi W Dryden (UTEP 9156), 21 mi N Dryden (MU 3042), 30 mi W Dryden (SRSU 1975), 20 mi W Langtry (KU 82338), 2 mi W Sanderson (SRSU 3016), 4.7 mi W Sanderson (TAIC 4352), 5.7 mi W Sanderson (UIMNH 34274), 7.9 mi W Sanderson (UTEP 9051), 7 mi SW Sheffield (TTU 2530), 10 mi S Sheffield (TNHC 7994), 13 mi S Sheffield (TNHC 7681), 21 mi S Sheffield (TNHC 8225), 25.9 mi S Sheffield (TCWC 28885), 30 mi S Sheffield (TNHC 7838); *Throckmorton Co.*, 15 mi SW Throckmorton (TNHC 26579); *Travis Co.*, no locality (LACM 103364), Austin (AMNH 4191, FSM 11989, TNHC 35221, TTU 86), NW of Austin (TNHC 26828), 7 mi SW Austin (FSM 56656–56658), 8 mi NW Austin (TNHC 2069), 10 mi N Austin (AMNH 122738), 12 mi W Austin (TNHC 19651, 20493), 15 mi SW Austin (TNHC 4497), 17 mi NW Austin (TNHC 4500), 18 mi NNW Austin (TNHC 4499), 20 mi NNW Austin (TNHC 4502), 20 mi W Austin (UIMNH 2652–2654), Gaines Ranch (TNHC 1847, 4897, 9084, 12295, 15295, 20542), Hamilton's Pool (LACM 66801), near Lake Travis (TCWC 20239), old river above Winfree (TNHC 29050), RR 620 1 mi W jct with RR 2769 (UAZ 25758), US 290 E of Hays Co line (FSM 7801–7802); *Upton Co.*, 24 km WNW Rankin (UTACV 14472–14474); *Uvalde Co.*, 3.2 mi S Nueces River on Hwy 55 (TCWC 64840), 8.2 mi N jct Hwys 1275 & 1835 (USL 19742); *Val Verde Co.*, Caulk Ranch (TAIC 3217), Comstock (TNHC 29047), N of Comstock on Pandale rd (Taic 4780), 1 mi W Comstock (ASC 9570, UAZ 40392), 1.5 mi SE Comstock (ASC 9568), 6.2 mi W Comstock (LSUMZ 23331), 7.9 mi NW Comstock (ASC 9565), 8 mi SW Comstock (USNM 32782), 15 mi SE Comstock (ASC 9564), 16.6 mi N Comstock (ASC 9571), 17 mi SE Comstock (ASC 9567), 18 mi SE Comstock (ASC 9569), 19 mi NE Comstock (TNHC 32512), 21.6 mi N Comstock (TNHC 32530), 7 mi NW Del Rio (UTACV 1339), 17 mi W Del Rio (MU 3041), 18 mi N Del Rio (CAS 103476), 18 mi NW Del Rio (SRSU 1843), 25.2 mi N Del Rio (UNM 8848), 36 mi NNW Del Rio (ASC 1524), 36.3 mi N Del Rio (UNM 8325), 40 mi N & 30 mi W Del Rio (ASC 5763), Devils River (USNM 32781), Evans Creek at Lake Amistad (SRSU 2746), 16.6 mi S Everett's Crossing (TAIC 4283), Fawcett Ranch (SRSU 3457, 3414, TTU 4355), 13 mi W Juno (ASC 9566), 2 mi W. Langtry (KU 61062), 7 mi N Langtry (TAIC 3558), 8 mi W Langtry (CM 88738), 20.9 km N Langtry (UTACV 14613), 25 mi N Langtry (TAIC 4118), 35 mi N Langtry (TAIC 3465 [3], 3476, 3498, 3556–3557, 3560, 3984), 29.8 mi W Loma Alta (TCWC 13837), Pandale hwy jct (TAIC 3540), 7.1 km S Pandale (UTACV 16341), mouth of Pecos River (UMMZ 74335–74336), Pecos River at Lake Amistad (SRSU 4812), US 90 at Pecos River (TAIC 1915, 2423, TCWC 33796, UMMZ 92798), US 90 2 mi W Amistad Dam (TAIC 2364), 1 mi W Shumla (TNHC 35223), Hwy 163 29 mi N jct with US 90 (UMMZ 175826), US 90 9 mi ESE Terrel Co line (UTEP 10576); *Williamson Co.*, 3 mi N Georgetown (UTACV 1340). **UTAH:** *Beaver Co.*, Baker's Canyon (USNM 36346), Beaver Creek hills (AMNH 29367–29368), Milford Valley, (BYU 564, 1640–1641), 50 mi W Milford BYU 563, 1637, 1809), White Sage Valley (SDNHM 40691); *Box Elder Co.*, Locomotive Springs (UU 917–918, 2000–2004, 8062), 22 mi N Wendover (BYU 42416); *Carbon Co.*, 25.3 mi S & 20 mi W Ouray (AMNH 112918), Price (BYU 2792, KU 82340, UU 1368, 1409–1410), 3 mi W Price (BYU 22951); *Davis Co.*, Antelope Island (LACM 121003), Farmington (AMNH 14231); *Duchesne Co.*, Montwell (BYU 16719), 5 mi W Roosevelt (BYU 16718); *Emery Co.*, Morrison Salt Wash 10 mi W Green River (AMNH 64840), San Rafael (BYU 2906), upper Temple Mtn (BYU 18997), 6 mi N Temple Mtn (BYU 20732), 2 mi NW Temple Jct (BYU 16614), Woodside (BYU 258), 2 mi NNE Jct Hwy 24 & road to San Rafael Swell (CAS 92465); *Garfield Co.*, Hog Springs (UTACV 12737), 4 mi NW Hog Springs (BYU 12694), 1 mi W Star Springs (BYU 12623); *Grand Co.*, Arches National Park (AMNH 115603, BYU 13036), near Castleton (LACM 103365–103366), 2 mi NW Castleton (UMMZ 68588), 25 mi N Cisco (FMNH 33909), 12 mi SE Cresent Jct (BYU 30533), near Colorado state line (KU 5533), Green River (BYU 257), 2 mi S Moab

(UMMZ 68587), 5 mi N Thompson (UMMZ 68586); *Iron Co.,* Antelope Springs (SDNHM 40662), Cedar City (BYU 392), 1 mi N Cedar City (KU 20906–20907), Sulphur Springs (SDNHM 40661); *Juab Co.,* 18 mi S & 9 mi W Eureka (CM 91197), 20 mi W Nephi (UIMNH 2135), Yopaz Mtn (BYU 9072); *Kane Co.,* 10 mi S Alton (BYU 11312), Glen Canyon (UAZ 39720), Kanab (UAZ 25759), 3 mi N Kanab (UMMZ 73390), 7 mi N Kanab (MNA 7.254), 19 mi E Kanab (BYU 8715), Kaiparowits Plateau (UU 1288, 1606), Orderville (SDNHM 25485), Piaria (BYU 2893); *Millard Co.,* Cove Fort (CAS 54150), 3 mi N Cove Fort (BYU 568), 20 mi NW Delta (SDNHM 674–675), 30 mi N Delta (CU 1082, SDNHM 1274), 65 mi W Delta (UIMNH 2132–2134), Fillmore (MCZ 13361–13362), 2 mi N Fillmore (UMMZ 70654), 10 mi NW Fillmore (UMMZ 70652), 10 mi SW Fillmore (UMMZ 70653), 10–11 mi W Fillmore (UMMZ 70655), 20 mi W Hinckley (BYU 16590), 7 mi S Kanosh (CAS 47756), Maple Grove Forest Canyon (UU 3386), 18.1 mi E NV state line (CM 49031); *Piute Co.,* 8.4 mi N Circleville (ASU 21199), 4.4 mi S Marysville (LACM 20590); *Salt Lake Co.,* 0.5 mi from mouth of Emigration Canyon (UU 14167), Fort Douglas (CAS 14167, 30923–30924, 38761), Salt Lake City (CU 3500, MCZ 8899, 9051, 9053); *San Juan Co.,* no locality (FMNH 25274, 25450, 25452, 25712, UTEP 5456), Bluff (AMNH 4871), 6 mi SW Bluff (CM 66658), Devils Lane near Needles (LACM 103367), Indian Creek (BYU 21709–21710), 6 mi W La Sal (BYU 18579), 25 mi SE La Sal (LACM 29037), 12 mi S Moab (UNM 6695), 36 km S Moab (KU 191935); *Sanpete Co.,* Ephraim (UU 89), Maple Canyon (UMMZ 64681); *Sevier Co.,* Monroe (SDNHM 38275); *Tooele Co.,* 13.8 mi N Bonnville Station (UU 5656–5657), 10 mi W Castle Cliff (CM 53604), Dugway Proving Ground (BYU 14823), 9 mi N Dugway Proving Ground entrance (LACM 103368), Gold Hill (BYU 2998), near Grantsville (UU 2478, 2482), W of Grantsville (UU 1966–1967), Lone Rock Skull Valley (LACM 121038–121080, MVZ 197596), between Ophir & Mercur (UU 2032), Stansbury Island (DURC 379 [2], LACM 121004, UU 1607), Stockton (SDNHM 24679), Tooele (UU 38), W of Vernon (UU 1219a, 8115), Wendover (LACM 24680), 14 mi N & 9 mi E Wendover (UU 3253); *Uintah Co.,* Dinosaur National Monument (BYU 10028), near Jensen (USNM 66196), LaPoint (MVZ 30256), 7 mi E Myton (KU 56097), Oil Town (BYU 22479), 10.6 mi S & 12 mi W Ouray (AMNH 112917), 29 mi S & 19 mi W Ouray (AMNH 112919), near Vernal (CM 7527), 10 mi N Vernal (MVZ 30255), 10 mi W Vernal (MVZ 30254), White River (CM 1430); *Utah Co.,* 3 mi S Allen Ranch (BYU 13042), Cedar Valley (BYU 216, 110, 1109, 14686–14687), Chimney Rock Pass (BYU 2842, 14685), Dividend (BYU 247), mtns W of Elberta (BYU 22093), 5 mi SW Goshen Bay (UIMNH 23875), Lake Mtn (BYU 386), W of Lehi (BYU 2779, 14684), Meseda Bench Prospect (BYU 14986), W of Meseda (UIMNH 34771–34772), Provo (FMNH 41680, UO 3687, USNM 8122), Rock Pile (BYU 30431), near Springville (AMNH 122735), Tintic (BYU 2031–2034, 2136, 2714), Utah Lake (LACM 121081, UU 881); *Washington Co.,* 16 mi NW St. George (USNM 44268), Snow Canyon (BYU 18967), Zion National Park (AMNH 63965, 64141, BYU 215, 394, 1098, 1399, 8739, CAS 56714, DMNH 4276, LACM 132466, SDNHM 3160, UU 74, 341, 805; *Wayne Co.,* no locality (FMNH 62895), Hanksville (BYU 8391–8392); *Weber Co.,* Ogden (MCZ 4595, USNM 10716); *County unknown,* no locality (ANSP 5363, MCZ 1943, USNM 14002), near Casisson, Colorado (KU 6668), Rush Lake (USNM 81244); **WASHINGTON:** *Walla Walla Co.,* 3 mi E Walla Walla (UMMZ 56952–56953). **MEXICO: CHIHUAHUA:** no locality (USNM 14272), 18.1 mi E Aldama (UNM 34249), 26.6 mi E Aldama (UNM 34248), 4.5 mi N Hwy 16 on E Colonias Access rd to Aldama (UNM 34250), 4.3 mi E jct Hwy 16 & 45 on 16 (UNM 34251), 18.6 mi W El Ancon (UAZ 35018), 13.6 mi N Ascensión (UAZ 36562), 5 mi N Camargo (UMMZ 117765), 5 km SW Chihuahua (CM 60003), 9.8 mi NW Chihuahua (UIMNH 46021), 30 km N Chihuahua (SDNHM 49501), 72 mi N Chihuahua (UTEP 4097), Coyame (UAZ 35017), 23.2 mi ENE Coyame (EAL 3489), Falomir (UIMNH 52432), 5 mi N Falomir (UIMNH 52433), 30 mi SW Gallego (MVZ 66116), 50 mi E General Trias (UNM 34247), 6 mi NE Janos (UTEP 4228), 5.2 mi S La Mula (SRSU 2816), Lago Santa Maria (USNM 46594), 30 mi N Las Delicias (CM 60006), Norogachi (AMNH 73752), 100 mi SSW Ojinaga (DMNH 2273), 13 mi N Pachera (MVZ 59286), Santa Barbara (AMNH 68193–68198, 68251, 68947–68950), rd to Santa Clara 12 mi from Hwy 45 (UTACV 4532), Sierra del Nido (MVZ 68873, 71014, 73053, UTEP 2519), 2 mi N Yepomera (UAZ 34783), 11.4 mi N Yepomera (UAZ 34425). **COAHUILA:** 3 mi E Americanos (KU 39567), Cuatro Cienegas (USNM 248109), 3 mi S Cuatro Cienegas (AMNH 77315), 3 mi W Cuatro Cienegas (TNHC 33012), 11 km SW Cuatro Cienegas (LACM 116256), 14 km S Cuatro Cienegas (CM 48192), del Carmen Mtns (FMNH 25300), 1 mi E tip San Marcos Mtns (KU 80282), San Pedro (MCZ 4582), 5 mi S San Pedro (USNM 105300), 11 mi N Zapata (UIMNH 48148). **DURANGO:** 8 mi W Durango (AMNH 102520), 84.8 mi W Durango (TCWC 33798), 41 mi E El Verfel (UTACV 8361), 27.5 mi S jct hwys 30 & 45 at La Zarca (UNM 33474), 3 mi SW Lerdo (AMNH 67326–67328), 13.3 mi W Mapuni (UTEP 7749), 4 mi E Metates (UTEP 9374), 3.8 mi NE Pedriceña (TCWC 44007), 6 mi NE Pedriceña (UIMNH 17857), 12 mi S Villa Ocampo (AMNH 86000). **JALISCO:** 8.1 mi ESE Tepetatillo (CAS 165260). **ZACATECAS:** 4 mi W Colorado (FMNH 106181), Sierra Organos (CAS 165223).

Masticophis schotti.—**UNITED STATES: TEXAS:** *Atascosa Co.,* Christine (UMMZ 74329), 4 mi

E Christine (SM 1760), 10 mi W Jourdanton (SDNHM 30412), 3.1 mi SE Kyote (TAIC 2229), Lytle (UIMNH 6299), near Pleasanton (TNHC 28758), 6 mi S Pleasanton (UMMZ 71341–71342), 9 mi E Pleasanton (CM 8457), 7 mi E Poteet (UMMZ 74068–74069); *Bee Co.*, Beeville (CA 10838–10840), 1 mi E Beeville (TNHC 28031), 6 mi S Berclair (TNHC 20403), 3.8 mi N Skidmore (TNHC 24445), Tulsita (TNHC 15294); *Bexar Co.*, San Antonio (ASC 4790, CM 16761, UMMZ 74071, UTEP 9931), near San Antonio (SDNHM 20970), 12 mi S San Antonio (UMMZ 74066), 12 mi S San Antonio (UMMZ 74330–74332), 16 mi E San Antonio (UMMZ 74327), 20 mi SW San Antonio (FMNH 108658), 20 mi S San Antonio (UMMZ 74070), Somerset (CM 19911); *Cameron Co.*, no locality (FMNH 38037), Brownsville (AMNH 24991, ANSP 22253, CAS 55354–55355, CU 1199, 1261–1262, FMNH 27170, KU 8393, MCZ 17998–18000, 46506, 15173, 62561 paratype, TCWC 65282, UIMNH 43493 paratype, UMMZ 57681 holotype, 57682–57684 & 57686–576894 paratypes, 59036, 60873–60876, USNM 75981, 84041, UU 1093–1095), 5 mi E Brownsville (TTU 5231), 10 mi NE Brownsville (UMMZ 74065), 12 mi NE Brownsville (UMMZ 74062–74064), 20 mi NE Brownsville (UMMZ 74073), 25–30 mi NNE Brownsville (AMNH 122736–122737), Harlingen (KU 8395), E Laguna Atascosa National Wildlife Refuge (LACM 59023), S Laguna Atascosa NWR (TCWC 61778), 33 mi NW hdqrs Laguna Atascosa NWR (USNM 238845), Laguna Heights (TAIC 4987), 3 mi NE San Benito (MVZ 78363), 3 mi S jct FM 106 & 1847 on 1847 (UTACV 8392); *Duval Co.*, 3.9 mi NE Benavides (LSUMZ 23333, 23337), 8.8 mi SW Benavides (23336), 1 mi W Freer (TAIC 2355), 1 mi N Freer (UMMZ 114405), 13.9 mi NE Freer (UMMZ 126173), 1.6 mi NE Realitos (LSUMZ 23339), 1.9 mi NW Realitos (LSUMZ 23334), San Diego (LSUMZ 23338, 23340), 7.9 mi SW San Diego (LSUMZ 23335), 4.7 mi jct 1329 & 2295 on 2295 (TAIC 3328 [2]); *Frio Co.*, Dilley (UTACV 293), 7 mi NW Dilley (TCWC 63774, 63919), 3.7 mi SW Moore (TNHC 47670), Hwy 57 at Frio River (USL 15084); *Goliad Co.*, 8 mi E Goliad (TNHC 17900, 17930); *Hidalgo Co.*, Alamo (USNM 159384), Edinburg (AMNH 74549–74551, CA 6350–6351), N of Edinburg (CU 589), 1 mi N Edinburg (TCWC 18301), 12 mi W Hidalgo (TCWC 65283), 13 mi N Edinburg (TCWC 36389), 19 mi S Encino (UIMNH 3832–3833), 14.7 mi NW La Joya (SM 8949), 6 mi S Linn (SRSU 2120), 6 mi S McAllen (TNHC 9059), 1 mi W Red Gate (TAIC 4666), 1 mi W jct FM 2984 & 676 (TAIC 1474); *Jim Hogg Co.*, 9.3 mi N Guerra (TCWC 60755), 2 mi S Randado (TAIC 4398), 5.8 mi S jct Hwys 3973 & 649 on 649 (TCWC 48658); *Jim Wells Co.*, Alice (TTU 791), 1.5 mi E Alice (UMMZ 69663), 3 mi S Ben Bolt (LSUMZ 13288), 5 mi S Ben Bolt (TNHC 23169), La Copita Experimental Ranch (TCWC 63408, 64389), 3 mi N Premont (UIMNH 16874), 10.9 mi N Premont (SM 8950); *Kenedy Co.*, 9 mi S Armstrong (TNHC 28003), 15.6 mi Armstrong (TAIC 3037), 12 mi S Norias (KU 61063), 10.2 mi S Riviera (FSM 43495), 5.7 mi S Sarita (TAIC 3099), 6 mi S Sarita (UTACV 16827), 8 mi S Sarita (LSUMZ 27724); *Kleberg Co.*, Laureles Division King Ranch (TAIC 5307), Kingsville (CAS 103473–103474, EAL 5000, TAIC 203, 361, 1707, 1731, 1942, 1976, 2059, 2073, 2382, 3563, 4255, 4772, 4857, 5257, 5307, 5364), 8.5 mi S Kingsville (TAIC 693 [2], 924, 2069), 2.5 mi S Riviera (TNHC 28030), 8 mi E Riviera (TAIC 933), 0.5 mi W Riviera Beach (TAIC 208); *Kinney Co.*, 2 mi W Bracketville (TNHC 42218), 5 mi WSW Bracketville (TNHC 47577), 5.9 mi E Bracketville (LSUMZ 32643), 9.9 mi W Bracketville (TCWC 63677), 13.6 mi E Spofford (TCWC 63918), 1.8 mi E & 4 mi S jct Rio Grande & Sycamore Creek (UTACV 7980); *LaSalle Co.*, Cotulla (CU 1760), between Encinal & Atlee on I-35 (TNHC 41907); *Live Oak Co.*, 13 mi SSE Campbellton (TCWC 14796), George West (TNHC 24492), near George West (TNHC 4306), 5 mi N George West (SM 8948), 3 mi W Three Rivers (TCWC 10587), 5 mi SSW Three Rivers (TNHC 25892), 0.3 mi S Whitsett (KU 145894–145895); *Maverick Co.*, Eagle Pass (USNM 1972 holotype), 1 mi W Quemado (UMMZ 113153); *McMullen Co.*, N McMullen Co (UMMZ 74333), 2 mi E San Miguel Creek on Hwy 173 (TNHC 28757), Tilden (CU 612), 25 mi S & 12 mi E Tilden (TNHC 47506), jct Hwys 624 & 16 (TAIC 2046); *Refugio Co.*, 3 mi W Woodsboro (DMNH 3070); *San Patricio Co.*, Aransas Pass (TAIC 3977), 1.5 mi NW Mathis (TNHC 24554), 2 mi N Mathis (TNHC 24567), 2.5 mi SE Mathis (TNHC 20406), 5 mi SW Mathis (TNHC 15301), 7 mi SW Mathis (TNHC 28362), along Nueces Bay (SDNHM 23190–23191), 1 mi S Sinton (FSM 22104), Welder Wildlife Refuge (MVZ 128099, TCWC 65281); *Starr Co.*, 10.4 mi S Agua Nueva (TCWC 63112), Falcon Heights (TCWC 51838), 5 mi W McCook (CAS 103475), 5 mi W Roma (TCWC 63111); *Val Verde Co.*, 2 mi W Del Rio (TNHC 42219), 2.5 mi W Del Rio (TNHC 42220), W Sacatosa Creek at Hwy 85 (CAS 9856); *Webb Co.*, 15 mi NNE Laredo (AMNH 126734), 37.8 mi NW Laredo (TCWC 42361), 4.1 mi W jct Hwys 44 & 83 on 83 (TAIC 733); *Willacy Co.*, 5 mi W Port Mansfield (TAIC 4072); *Zapata Co.*, no locality (TNHC 23182), 1 mi NE Escobas (TCWC 48657), 5.3 mi S Laredo (UMMZ 74067), along Rio Grande (UMMZ 92797), 6 mi N San Ygnacio (TCWC 36388), 8.4 mi NE San Ygnacio (UTACV 10438); *Zavala Co.*, 5.4 mi S & 6.2 mi E LaPryor (TCWC 64997). **MEXICO: COAHUILA**: 3 mi E Muzquiz (KU 38331), 20 mi E Nava (KU 39960), 18.5 mi SE Saltillo (EAL 3377), 3.4 mi S Villa Union (SDNHM 49792). **GUANAJUATO:** Guanajuato (USNM 10240), Hwy 57 at San Luis Potosi state line (TCWC 65903). **HIDALGO:** Ixmiquilpan (AMNH 72422), 77 km N Ixmiquilpan (ANSP 28689), 8.3 mi N Jacala (UMMZ 106396), 12 mi S Jacala (UAZ 27006), 5 km S Venados (SDNHM 58399), 9 km S Zacualpan

(TTU 6800), 11 km S & 1 km W Zacualpan (TTU 6799), 2 mi W Hwy 85 at S entrance to Zimipan (LACM 128447). **MICHOACAN:** 2 mi W Morelia (MVZ 78364), Tacicuaro (FMNH 100296, USNM 111312). **NUEVO LEÓN:** 4 mi W Allende (KU 68117), Aramberri (KU 87748), 10.4 mi W Cerralvo (EAL 3571), 12 km E & 15 km S Galeana (TU 17551–17552), 1 mi E Iturbida (TCWC 30430), 2 mi S Linares (AMNH 69938), 19 km N & 9 km E Matehuala (FWM 7255), 4 mi S Monterrey (TU 17547), 13 mi E Monterrey (MCZ 46321), 25 mi S Monterrey (UIMNH 3836), 24.8 km S Sabinas Hidalgo (TCWC 60760–60763). **QUERÉTERO:** 6.3 mi El Madroño (TCWC 29489), 0.2 mi E Jalpan (TCWC 32928), km 106 on rd from Jalpan to San Juan del Rio (MCZ 157827), 1 mi N Peña Blanca (TCWC 45658), 8 km N Querétero (SDNHM 49502), 6.4 mi NE San Juan del Rio (TCWC 38459), 1 mi E San Pablo Jct (TCWC 53061), 1 mi NW Toliman (TCWC 41012). **SAN LUIS POTOSI:** Alvarez (MCZ 19024, 19028–19031, 46452), Bledos (LSUMZ 4204), between Charcas & Venado (UMMZ 77245), 7.5 mi N El Valles (AMNH 67160), La Naranja (TU 17562), 8 mi NE Maíz (AMNH 110413), 13 mi E Maíz (AMNH 85246), 35 km W Maíz (UIMNH 17858), 30 mi NW Maíz (MVZ 129331), 10 mi E Matehuala (CM 60004), 20 mi S Matehuala (AMNH 93427), 24 mi S Matehuala (EAL 24), 38 km SW Rio Verde (LSUMZ 5396), 8.5 mi SW San Luis Potosi (UMMZ 120221), 12.7 mi SW San Luis Potosi (FWM 8670), 43.4 km E San Luis Potosi (UTACV 12365), 4.5 mi NNW Santo Domingo (EAL 4201). **TAMAULIPAS:** 4 mi E Aldama (UMMZ 101260), 50 mi S Brownsville (USNM 64681), 25 mi N El Limon (UMMZ 102898), 1 mi S Fortuna (UMMZ 110956), 1.3 mi N Gomez Farias (SM 11425), 4.3 km S Gomez Farias (UTACV 16135), 3 mi N Gomez Farias (SM 8947), Juamave (UMMZ 95204), La Joya de Salas (UMMZ 110818), 29 km N Mante (UMMZ 143724), 27 mi N Mante (UIMNH 3831), Matamoros (USNM 1974), 25 mi SW Matamoros (KU 61064), Miquihuana (MCZ 19552–19553), 11.7 km NW Morales (TNHC 28899), 8 km S Nuevo Laredo (UTACV 12364), 0.3 mi SW Rancho Carricitos (TCWC 49933), 12 km SE Reynosa (UMMZ 143723), 20 mi ESE Reynosa (MVZ 36748), Soto La Marina (USNM 37546), Victoria (AMNH 75935), 7 mi N Victoria (MCZ 46322), 15.5 mi SW Victoria (UMMZ 114675), 22 km N Victoria (USNM 111279), 18 mi SW Victoria (AMNH 104465), 63 km E Victoria (TCWC 26730), 3 mi N Villagran Monterrey (TNHC 32323), 1 mi S jct Hwy 101 & San Carlos rd (FSM 42308). **VERACRUZ:** 9 mi SE Jalapa (UO 33467), 35 mi S Nautla (TAIC 2648).

Masticophis taeniatus × *M. Schotti.*—**UNITED STATES: TEXAS:** *Uvalde Co.,* 13 mi N Uvalde (TCWC 49204); *Val Verde Co.,* 8.5 mi NW Del Rio on US 90 (CAS 9864), mouth Pecos River (UMMZ 74334). **MEXICO: COAHUILA:** del Carmen Mtns (FMNH 25301), 14.2 mi N Saltillo (TCWC 54321–54322). **NUEVO LEÓN:** 20 mi SSW Galeana (FWM 7931), 5 mi E San Roberto (ANSP 28688).

Masticohpis bilineatus.—**UNITED STATES: ARIZONA:** no locality, (ANSP 5362); *County unknown,* Colorado Bottom (USNM 1981); *Cochise Co.,* Bisbee (BYU 256), 25 mi W Bisbee (CA 7809), 30 mi W Bisbee (CA 7470), 6 mi SSW Carr Canyon (AMNH 84969), Chiricahua Mtns (AMNH 75361, CU 10679, LSUMZ 8799, MVZ 7943, 8193, 44932, 97078, TCWC 63048, UMMZ 114130, UTEP 2824, 9592), 1 mi N Dox Cabezos (MVZ 6942), 15 mi S Ft Huachuca (UIMNH 6062), Huachuca Mtns (ANSP 16488, BYU 30029, 31880, MCZ 11409, MVZ 5406, 44742), Portal (AMNH 80816, 91620–91621, 109438–109439), 0.5 mi E Portal (CU 10660), 0.4 mi S & 0.8 mi W Portal (AMNH 11159), 1 mi SW Portal (AMNH 84972, 99333, CM 66092), 1.5 mi E Portal (MVZ 137578), 2 mi W Portal (CA 5070), 2 mi S Portal (CM 66057), 2 mi E Portal (LACM 2257), 3 mi W Portal (AMNH 91622), 3.5 mi SW Portal (ASC 6597), 4 mi NW Portal (UMMZ 121839, 121917), 5 mi W Portal (UMMZ 114633), Southwestern Research Station-SWRS (AMNH 80817, 84971, 111193–111194, 123866, FSM 8690, LACM 2255, MVZ 67188, 67204), 0.25 mi W SWRS (AMNH 84970), 2.5 mi W SWRS (LACM 133880), 3.4 mi S Silverspur (UIMNH 72001), Tombstone (CU 2320), 20 mi W Willcox (CA 16456); *Gila Co.,* no locality (USL 18840), 2 mi NW Coolidge Dam (UMMZ 114634), 20 mi N Globe (TNHC 16793), Roosevelt Lake (USL 8408), 8 mi S Salt River (ASU 1716), 10 mi N Salt River on Hwy 60 (CA 9520), Salt River Canyon (ASU 10536–10538), Sierra Ancha Experimental Forest (CM 51907–51908); *Graham Co.,* 5 mi SE Bonita (ASU 7030), Camp Grant (USNM 8434), 0.25 mi S Cyclone (UIMNH 24555), Gila River Sec 28 T6S R28E (CM 70672), Marijilda Base Camp (ASU 7020, 7032–7033), 3 mi E Marijilda Base Camp (ASU 7014), Marijilda Canyon (ASU 7770, CM 48661, 51492, 70891, 70900, 70933, 70944), Pinaleno Mtns (CA 17006, CM 69819, 71041, 71067, 71254, 71537, 71629, 71667, 107289), 11 mi SW Safford (CA 11083), 11 mi S & 4.5 mi W Safford (ASU 7011, 7017), 25 mi W Safford (CA 12974), 30 NW Safford (UIMNH 71999-72000), Mt Turnbull (USNM 54719), 5.4 mi SW jct Hwys 366 & 666 on 366 (UTEP 9545); *Greenlee Co.,* Eagle Creek (CM 71184, 70746), Gila River (CM 71425); *Maricopa Co.,* 10–20 mi N Ajo (ASU 13846), 11 mi N Apache jct (CM 48620), Ashdale Ranger Station (USL 6724), 7.8 mi ENE Carefree (CM 69160), Cave Creek (ASU 753), E of Mesa (ASU 59), Morristown (SDNHM 8414), 4.8 mi N Morristown (CA 16158), 1 mi N Sunflower (ASU 3686), Tortilla Flats (ASU 9085, CAS 80670), 5.5 mi SE Wickenburg (UIMNH 71996–71997), 7 mi SE Wickenburg (UIMNH 71998); *Mohave Co.,* 15 km W Bagdad (ASU 14488), Hwy 93 at mile post 157.7 (ASU 22134); *Pima Co.,* 0.5 mi S Ajo (UAZ 36767), 2 mi W Ajo (UAZ 40028), 24 mi S Ajo (NMSU 2634), Kitt Pk Observatory (UAZ 25158), 1.3 mi E jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 32787), 2.8 mi from Hwy 86 & Kitt Pk Rd on 86 (UAZ 20794), 3.2 mi E jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 20756), 3.6 mi from jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 20796), 4.1 mi E jct Hwy 86 & Kitt Pk Rd (UAZ 20795), 7.3 mi from jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 20786), 3.7 mi below jct Kitt Pk Rd & Picnic Area Rd (UAZ 20783), Organ Pipe Cactus National Monument (CM 48524, UIMNH 5611), 0.5 mi from Pima Canyon mouth (TCWC 30720), 22.9 mi W Robles Jct (UAZ 20799), Sabino Canyon Rec Area (INHS 7571, 8007), Santa Rita Mtns (MU 2494), Sells (FSM 56664), 8 mi N Sonoita (UAZ 36250), 8.7 mi N Sonoita (UAZ 20765), 15.2 mi N Sonoita (UAZ 34699), 8 mi N Tanque Verde Rd on Mt Lemon Rd (MVZ 180258), 14 mi N Tucson (CA 3929), 50 mi S Tucson (EAL 883); *Pinal Co.,* 30 mi S Phoenix (CA 16157), Picket Post Mtns (CA 9825), Superior (ASU 1622, CA 9525, 9680), 5 mi W Superior (CA 13579–13580), 6 mi E Winkleman (UIMNH 37712); *Santa Cruz Co.,* 7.7 mi W Ft Huachuca (UTEP 11162), 8.9 mi WNW Lochiel (LSUMZ 40983), Patagonia (CU 5234), 3 mi S Patagonia (CU 5492), 2 mi SE Ruby (LSUMZ 32900), 8.8 mi W jct Hwys 89 & 289 (EAL 2770), 9.8 mi S Jct Hwys 82 & 83 on 83 (TCWC 63379); *Yavapai Co.,* Bradshaw Mtns (AMNH 63977), 2.2 mi NE Hillside (BYU 37042). **NEW MEXICO:** *Hidalgo Co.,* Adobe Creek center Sec 24 T31S R19W (AMNH 77453), Animas Mtns (AMNH 84976, 87276, UNM 6979), 8 mi W Animas (AMNH 84974–84975), 8.5 mi S & 2 mi W Animas (NMSU 6395), 3.5 mi W Cloverdale (UNM 8298), 7.5 mi NW Cloverdale (LACM 2253), 10.5 mi N & 13.5 mi E Cloverdale (UTEP 1344), 16 mi NE Cloverdale (CM 18222), Guadalupe Mtns (UNM 3334, 6786, 8297), Indian Creek Canyon (UNM 13820), Peloncillo Mtns (AMNH 75949–75950, 119512, UNM 7687), 7 mi S Rodeo (MVZ 67203), 8 mi SSE Rodeo (CU 5768), 17 mi N & 3 mi E Rodeo (UNM 39100), San Geronimo Trail 5 mi E AZ state line (LACM 2254), 2 mi SW Steins (LSUMZ 8806), 8.2 mi S jct Hwys I-10 & 80 on 80 (LACM 76563), SW 0.25 Sec 15 T34S R21W (UNM 32349). **MEXICO: AGUASCALIENTES:** 2 km W Calvillo (UTEP 7747), 4.5 mi E Calvillo (LSUMZ 35033). **CHIHUAHUA:** near Batopilas (USNM 46382). **COLIMA:** no locality (MCZ 11409), Colima (AMNH 19636). **DURANGO:** Santa Ana (KU 74567), 2 km E Villa Corona (UTEP 3977). **JALISCO:** 2 mi E Bolanos (KU 91424), 10.1 km SW Cocula (TCWC 48059), Guadalajara (USNM 32212), 4.8 km S Huejucar (KU 102966), Hwy 15 S of Lago de Chapala (TCWC 33793), 5.3 mi S Nayarit state line near Ixtlan del Rio (UIMNH 40361), 13 mi N Sayula (AMNH 93339), 4.8 km E Totatiche (KU 100512), 10 mi NE Union de Tula (MVZ 7220). **NAYARIT:** 17.9 mi SW Acaponeta (FSM 24761), 11.4 mi S Acaponeta turnoff (LACM 6990), Jesus Maria (AMNH 74953–74956), between Marquezado & Auzata (AMNH 19640), 15 mi E San Blas (UIMNH 71988), Hwy 15 near Sinaloa border (LACM 6989), 2.4 mi N Tecuala turnoff (UIMNH 85728), Tepic (USNM 46417), rd from Tepic to Paga (LACM 8739). **OAXACA:** Cuicatlam (USNM 46499). **SINALOA:** 4 mi S Casa Blanca (KU 83406), 0.2 mi W Concordia (LACM 6992), 10 mi W Concordia (UMMZ 102483), 15.6 mi N Culiacan (UIMNH 71992), 37.5 mi N Culiacan (UIMNH 71991), 72 mi S Culiacan (FSM 42096), Elota (UIMNH 83457), 12 mi N Escuinapa (UIMNH 41593), 17.2 mi NW Escuinapa (TNHC 25475), 30 mi S Escuinapa (UIMNH 71994), Isla Palmito del Verde (KU 73569–73570), 15 mi N Los Mochis (CM 54004), Mazatláan (TCWC 21903), 1.1 mi N Mazatlán (UIMNH 83456), 15.8 mi N Mazatlán (LACM 103106), 26.8 mi N Mazatlán (LACM 103104), 29 mi N Mazatlán (UIMNH 71989), 52.4 mi N Mazatlán (UIMNH 71900), Hwy 15 5 mi N Nayarit state line (LACM 6991), Rosario (KU 73568), San Ignacio (LACM 6986), Terreros (LACM 6993), 8 km N Villa Union (KU 80757), 5.8 mi NW Villa Union (CAS 24114), 18 mi SW Villa Union (CAS 120883), 34 mi NE Villa Union (LACM 103105), 6.2 mi N & 10.6 mi E jct Hwys 40 & 15 (CAS 23954-23955). **SONORA:** no locality (ASU 8421), 47 km E Agua Prieta (UTACV 17796), Alamos (MCZ 43251), W of Alamos (CAS 140518), 1 mi W Alamos (LACM 103109), 2 mi SSE Alamos (LACM 103107), 4 mi W Alamos (LACM 103108), 7 mi W Alamos (ASU 6037–6038, 6454, 6645), 17 mi W Alamos (ASU 6510), 17 mi S Casa Blanca (MVZ 67430), 0.4 mi NE El Coyote (MVZ 136780), S El Novillo 9MVZ 136781), Guaymas (MTKD 15068 paratype, 15523 holotype, USNM 15880), 4 mi SW Guaymas (KU 48919–48920), Guirocoba (AMNH 63722–63723, MVZ 50793–50796), 5 mi S Hermosillo (UMMZ 72103), 5 mi SW Hermosillo 9FMNH 102669), 32 mi SE Hermosillo (AMNH 84978), Isla San Esteban (KU 91587, LACM 20601–20604, 74047, MVZ 74954–74956, 76499, SDNHM 3826, 40855, TTU 8017, UMMZ 128928), Isla San Pedro Martir (UO 32528), Isla Tiburon (USNM 222054–222058), 5 mi SE La Pintada (AMNH 80815), La Posa (FMNH 102670, UIMNH 17838), Las Chispas (AMNH 3469), 25 mi W Maxatan (AMNH 84977), San Luis Mtns (USNM 21053–21054, UTACV 17794–17795), 4.5 mi S Tubutama (CAS 16642), 5 mi S Tubutama (CAS 17297), between Vicam & Guaymas (LACM 103110). **ZACATECAS:** 9 mi SSW Jalpa (UTEP 7748), 1.7 mi N Los Bajios (LSUMZ 26233), San Juan Capistrano (USNM 46481), 7 km S Santa Rosa (UTEP 3978), Zapogui (USL 12283).

APPENDIX 2

Electrophoresis Samples

Masticophis bilineatus.—**ARIZONA:** *Cochise Co.* (TCWC 63696); *Pima Co.* (TCWC 64995). **NEW MEXICO:** *Hidalgo Co.* (TCWC 64842).

Masticophis s. schotti.—**TEXAS:** *Frio Co.* (TCWC 63774, 63919); *Jim Wells Co.* (TCWC 64839); *San Patricio Co.* (TCWC 65281); *Zavala Co.* (TCWC 64997).

M. s. ruthveni.—**TEXAS:** *Cameron Co.* (TCWC 65282); *Hidalgo Co.* (TCWC 65283). **MEXICO: GUANAJUATO:** (TCWC 65903).

Masticophis t. taeniatus.—**IDAHO:** *Ada Co.* (TCWC 64836–64837). **NEW MEXICO:** *Catron Co.* (TCWC 65001); *Hidalgo Co.* (UTEP 11355); *Sierra Co.* (NMSU uncatalogued); *Socorro Co.* (TCWC 66165).

M. t. girardi.—**TEXAS:** *Brewster Co.* (TCWC 64999, 65285); *Edwards Co.* (TCWC 65923); *El Paso Co.* (TCWC 64998, UTEP 10804); *Kimble Co.* (TCWC 64809, 65284, 65287); *Llano Co.* (TCWC 63772–63773, 63876, 64841, 64996, 65000); *McCulloch Co.* (TCWC 64838); *Medina Co.* (TCWC 63775); *Presidio Co.* (TCWC 64810–64811, 65286); *Uvalde Co.* (TCWC 64840).